THE HYOBRANCHIUM AND THROAT MYOLOGY
OF THE ADULT AMBYSTOMIDAE OF THE UNITED STATES
AND NORTHERN MEXICO

by

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and

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ABSTRACT

The 16 species and subspecies of the Ambystomidae of the United States are placed into six groups according to their throat morphology as follows: The *Dicamptodon* group, the *Rhyacotriton* group, the *A. Annulatum-A. cingulatum* group, the *A. gracile-A. jeffersonianum-A. mabeei-A. macrodactylum-A. maculatum* group, the *A. talpoideum* group, the *A. opacum-A. texanum* group, and the *A. rosaceum-A. t. tigrinum-A. t. melanostictum-A. t. nebulosum* group. *Dicamptodon* appears to be the most primitive group and *Rhyacotriton* the most specialized. Based on the morphology of the throat region it is suggested that *A. rosaceum* be placed in the tiger salamander group as a subspecies of *A. tigrinum*.

The results of this investigation support the hypothesis that Ambystomidae is primitive to Salamandridae and to Plethodontidae. The findings which have led to this conclusion are based upon the protrusibility of the tongue, and upon the structure and presence of the epibranchial, otoglossal, second radial, and second basibranchial cartilages of the three families.

INTRODUCTION

The ambystomid salamanders are strictly North American in distribution, ranging from southern Alaska and extreme southern Labrador in the north to the southern parts of the central Mexican Plateau. Most salamander taxonomists recognize five living genera—*Dicamptodon*, *Rhyacotriton*, *Rhyacosiredon*, *Ambystoma*, and *Bathysiredon*. Two of these, *Rhyacosiredon* and *Bathysiredon*, are found only in Mexico. *Dicamptodon* and *Rhyacotriton* are found along the Pacific Coast of the United States, and the genus *Ambystoma* is essentially coextensive with the entire family range. This study deals with the ambystomids of the United States, plus one Mexican species *Ambystoma rosaceum*. There are about 30 species in the entire family, and of this number 13 are found within the boundaries of the United States.

Most workers believe that *Dicamptodon* and *Rhyacotriton* are related and differ from *Ambys-* *toma* in certain features. Tihen (1958) subdivides the genus *Ambystoma* as follows: (An asterisk following the name indicates that it is found in the United States.)

Subgenus: Ambystoma

The mexicanum group
  Ambystoma kansense
  Ambystoma lermaensis
  Ambystoma mexicanum

The tigrinum group
  Ambystoma amblycephalum
  Ambystoma bombypellum
  Ambystoma fluvinatum
  Ambystoma granulosum
  Ambystoma hibbardi
  Ambystoma lacustris
  Ambystoma ordinarium
  Ambystoma rosaceum
  Ambystoma subsalsum
  Ambystoma tigrinum°

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The opacum group
  Ambystoma opacum°
  Ambystoma talpoideum°

The maculatum group
  Ambystoma gracile°
  Ambystoma jeffersonianum°
  Ambystoma laterale°
  Ambystoma macrodactylum°
  Ambystoma maculatum°

Subgenus: Linguaelapsus
  Ambystoma annulatum°
  Ambystoma cingulatum°
  Ambystoma mabeei°
  Ambystoma schmidti
  Ambystoma texanum°

Subgenus: Bathysiredon
  Bathysiredon dumerili

Tihen (1958) has suggested that the family Ambystomidae had its origin in the late Mesozoic and was probably derived from Asiatic hynobiids. He further suggests that *Dicamptodon* and *Rhyacotriton* were established in the western part of the continent at this early date, and that the remainder of the family had its beginning at a later date in the northeastern part of the continent.

There is a lack of agreement among taxonomists as to the relationships of the various families of salamanders. Some investigators (Dunn, 1926; Noble, 1927) consider the Ambystomidae to be primitive in relation to the Salamandridae and seem to be convinced that the Plethodontidae can be derived from the Salamandridae, whereas others (Regal, 1966; Bishop, 1943) would derive them from the Ambystomidae. The primary objective of this study has not been to help resolve this question, since our studies are directed primarily at the generic and species levels. However, the data do suggest certain conclusions pertaining to interfamilial relationships, and these are discussed later in the paper.

Inasmuch as this paper is concerned only with the hyobranchial apparatus and the myology of the throat, it contains some inherent limitations, and the conclusions which will be drawn are subject to modification based on evidence from other sources.

One of the first workers to study the anatomy of the throat region in ambystomid salamanders was Cope (1887). The findings of several subsequent workers were later summarized by Piatt (1940). With respect to certain structures, our observations do not agree with those made by these earlier workers, as will be pointed out hereinafter.

Other nonanatomical approaches to the study of amphibian evolution have been made in the past. Some investigators (Boulenger, 1910; Sampson, 1900; Brandes, 1901; Kerr, 1919; Barbour, 1926) have used developmental patterns in the study of amphibian evolution. Noble (1927) contends that, while habits are changeable among the higher vertebrates, they are the direct result of inherited organization in the lower vertebrates, and he suggests that these habits may even be more stable than many structural features in these lower forms. Accordingly, he has used courtship behavior extensively, based on the premise that the more specialized the behavioral pattern the greater the probability that it will be found only in closely related forms.

One of the obvious manifestations of the process of evolution is the series of anatomical changes in a group of organisms which accompany and reflect the changes that occur in the environment.

The throat region is a fruitful area of anatomy on which to study salamander evolution since it is involved in both feeding and breathing mechanisms. Feeding structures associated with the aquatic habitat are notably different from those found in terrestrial forms. Terrestrial forms are unable to utilize water for the capture, manipulation, and softening of food items, but they have evolved instead a tongue to accomplish these purposes in a terrestrial environment.

Regal (1966) has used tongue structure in the classification of terrestrial salamanders. He describes the aquatic tongue as consisting of a mere thickening of the mouth floor around the branchial elements. He groups terrestrial tongues into three types based on their freedom from the floor of the mouth, and the ability to extend the tongue out of the mouth by means of the hyoid elements. The ambystomids have a terrestrial-type tongue that is free at the lateral and posterior margins but is not as protrusible as the tongue found in the Salamandridae and the Plethodontidae. As a result of this structure, the ambystomids are restricted to larger food items. Salamanders with the more advanced tongues are able to flip the tongue out of the mouth to catch small, elusive insects, and, in addition, they are able to use the more conservative methods for the capture of larger food items.

Some of the other structures which are also associated with feeding and breathing mechanisms that have been studied by various workers include teeth, skull bones, and vertebrae (Tihen, 1958); the direction of tooth replacement

(Regal, 1966); and the hyobranchial apparatus (Cope, 1887; Smith, 1920; Francis, 1934; Tanner, 1952; Wake and Özeti, 1969).

The present study is based exclusively on the dissection of adult salamanders. Larval forms have been avoided owing to the great variability that exists in their development. Brandon (1961) points to the fact that earlier workers had concentrated their descriptions on either newly hatched or fully grown larvae but that nothing was known for many of the intermediate sizes. He prepared a table based on balancers, limbs (buds and toes), and skin pigmentation to be used to identify all sizes of larvae.

Dunn (1940), in his paper on the races of *Ambystoma tigrinum*, makes the statement that larvae and recently transformed young are usually useless in racial discrimination. Furthermore, the anatomical changes that occur at metamorphosis are rather extensive, and the adult stage of development, therefore, appears to be the most reliable ontogenetic level at which an anatomical investigation could be undertaken. For a quantitative treatment of the changes in weights and in linear measurements of the body and organs that occur at metamorphosis, the reader is referred to Latimer and Roofe (1964).

Inasmuch as we have considered in this paper only those ambystomids that normally occur in the United States (with the exception noted above), the question of neoteny does not concern us. On the other hand, a complete treatment of the family would include specimens from populations in which there is complete or partial neoteny, and an investigator undertaking such a study would be forced to compare gilled animals with nongilled forms. Complete neoteny is found in populations of the *tigrinum*, *mexicanum*, and *Bathysiredon* groups of Tihen (1958), and partial neoteny is found throughout the family.

We have been able to confirm the platelike otoglossal cartilage of *Dicamptodon* as reported by Cope (1887), but our findings concerning this structure in *Ambystoma gracile* and *A. texanum* do not agree with his observations. The otoglossal cartilage in these latter two species is not platelike as in *Dicamptodon* but is annular in shape.

We have found the otoglossal cartilage to be of special importance in the process of feeding. The vomerine teeth are located on the roof of the mouth directly opposite the otoglossal in the Ambystomidae, and this cartilage appears to function as a rod with which to impinge food against these teeth. The otoglossal is either absent or drastically reduced in the Salaman-

dridae and Plethodontidae, and the vomerine teeth in these two families do not form a transverse series opposite the position of the otoglossal as in the Ambystomidae, but tend rather to be scattered throughout the mouth. The salamandrids and plethodontids use the entire tongue to press food up against their teeth, whereas the ambystomids with their rather immovable tongues rely heavily on the otoglossal cartilage for this purpose.

We have found, contrary to the statements of earlier workers (Tihen, 1958, for example), that the majority of the hyobranchium in *Dicamptodon* is not solidly ossified, but rather is mostly cartilaginous. The only structures which are solidly ossified in *Dicamptodon* are the tips of the ceratohyals and the epibranchials. The second basibranchial cartilage is partially ossified in most of the specimens studied, but in a few of them it was completely cartilaginous. An epibranchial cartilage, the presence of which is considered to be primitive (Özeti and Wake, 1969), was observed in all of the specimens we have studied. The first basibranchial cartilage and also the ceratohyal are primitively ossified, and they were at least partly ossified in most of the species observed in this study.

For the most part, the muscle terminology we have used is in agreement with that suggested by Drüner (1901), Francis (1934), Edgeworth (1935), and Piatt (1939). We have used the name *interhyoideus posterior* for the most posterior of the ventral hyoid constrictors, and we agree with Piatt (1940) that the terms *gularis* and *quadratopectoralis* should be used only in the Plethodontidae. Piatt has also stated that the subhyoideus is a special anterior derivative of the interhyoideus, and that no such muscle exists in the Ambystomidae. In all of the specimens we have observed, however, this muscle is present, extending forward from the posterior tip of the ceratohyal to join the fibers of the interossaquadrata near the midline of the throat. In *Rhyacotriton*, the subhyoideus inserts even further forward along the posterior edge of the mandible.

Previous studies on the hyobranchial apparatus and throat myology of the ambystomid salamanders have been sketchy and incomplete. The families Salamandridae and Plethodontidae have been studied relatively recently (Piatt, 1935; Hilton, 1947a; Hilton, 1947b; Tanner, 1952; Özeti and Wake, 1969) and rather completely, but the same cannot be said for the Ambystomidae. It has been this need for further study which has provided the major stimulus for this investigation.

MATERIAL AND METHODS

The materials which have been used in this study were made available for dissection by the Brigham Young University Natural History Museum, California Academy, Museum of Natural History, U.S. Natural History Museum, and from museum collections of other universities throughout the United States. Numerous specimens were also obtained from the field collections of private individuals. Specimens of the Ambystomidae which we dissected are: *Dicamptodon ensatus, Rhyacotriton olympicus, Ambystoma rosaceum, A. tigrinum, A. opacum, A. talpoideum, A. gracile, A. jeffersonianum, A. macrodactylum, A. maculatum, A. annulatum, A. cingulatum, A. mabeei,* and *A. texanum.* We have also dissected the subspecies *A. t. tigrinum, A. t. nebulosum,* and *A. t. melanostictum* of the tiger salamander. For comparison we also dissected one specimen of *Salamandra salamandra.*

In the case of some species there were as few as two specimens available for dissection, and in the case of the Long-toed Salamander, *Ambystoma macrodactylum,* only one was available. We have therefore made no attempt to ascertain the degree of individual variation within each species. In making some conclusions concerning phylogeny, we have attempted to use morphological structures which tend to have low variability between individuals of the same species. All of the dissections were performed with the aid of a stereoscopic microscope at magnifications varying from 10 to 30 diameters. All measurements were made with calipers to one-tenth of a millimeter.

The origin, insertion, size, and shape of thirteen muscles are described in detail for each specimen, and the hyobranchium is, likewise, described for each. The percentages of ossification and/or chondrification for the various elements of the hyoid apparatus are mentioned and their significance in determining phylogeny is discussed.

Since most of the muscles are bilaterally symmetrical, two depths are shown on some illustrations in order to reduce the number of drawings. All of the descriptions and illustrations have reference to adult specimens. Eosin dye was used only occasionally to distinguish muscular from connective tissue on very small specimens. A few specimens were also cleared according to the Schultz-Potash technique as modified by Hansen and Tanner (1958) and then stained with alizarin red and stored in glycerin. The majority of the specimens have been preserved in 60 percent alcohol and have been accessioned in the collections of the Museum of Natural History at Brigham Young University in Provo, Utah.

We have selected 48 morphological characters, and have used them in the deduction of a phylogeny for the genus *Ambystoma* according to the method of Wishart (1969). The morphology which is included in this paper includes information on feeding and breathing structures, and does not attempt to include any of the numerous other body systems or information concerned with life history. The reader is therefore reminded as to the limitations of this work, and he is advised that the findings discussed herein be used in conjunction with information from other sources in the final decisions concerning relationships of the Ambystomidae.

GENERAL FEATURES OF THE HYOBRANCHIAL SKELETON

There has been considerable controversy concerning the terminology of the hyobranchial skeleton, as evidenced by the large amount of synonomy which exists in the literature at the present time. We have followed Wiedersheim (1877), Noble (1931), Piatt (1935, 1938), Tanner (1952), Wake (1963, 1966), and Özeti and Wake (1969) as far as hyobranchial skeleton terminology is concerned. We use the terms ceratobranchial rather than hypobranchial, epibranchial rather than ceratobranchial, first basibranchial rather than copula or basihyal, second basibranchial rather than os triangulare, and radial cartilages rather than cornua.

In larval forms, the hyoid arch is present as well as portions of four branchial arches. Following metamorphosis, however, there is a reduction of both the hyoid and branchial arch components, leaving only portions of the hyoid arch and the first two branchial arches in the adult. The majority of these structures is usually cartilaginous with centers of ossification most commonly occurring in the center of the first basibranchial, the tips of the epibranchials, the posterior tips of the ceratohyals, and the medial portion of the second basibranchial.

The first basibranchial cartilage is the main supporting element inasmuch as it provides a base of attachment for most of the other components. It is located in a midventral position, and the central portion is usually ossified, as mentioned above. Özeti and Wake (1969) indi-

eated that the shape of the first basibranchial was characteristic of each genus in the Salamandridae, and it appears that the same trend can be found in the genera of ambystomids presented in this paper. In *Dicamptodon* this structure is truncate, in *Rhyacotriton* it is shaped like an elongated pear, and in *Ambystoma* it is either pear-shaped or shield-shaped (Fig. 1-16).

In adults, the hyoid arch consists of two elements on each side — the first radial cartilage and the ceratohyal. In the larval stage, these two structures articulate with each other, but in the adult condition they are often separated or attached by way of a ligament. The first radial cartilage attaches to the anterior edge of the ceratohyal. There are no muscles which attach to these first radial cartilages. The anterior end of the ceratohyal is flat and spatulate in shape while the posterior end becomes rounded in cross section and curves dorsally to attach to the quadrate by way of the hyoquadrate ligament. The anterior end serves as an attachment point for the subarcualis rectus I, and the posterior end is the point of origin for the subhyoideus. In the majority of specimens observed, the posterior tip of the ceratohyal was ossified. Özeti and Wake (1969) report that from one-half to two-thirds of the ceratohyal is ossified in salamandrids, and Tanner (1952) reported a complete lack of bone in these structures in the plethodontids which he studied.

The two second radial cartilages arise from the sides of the first basibranchial and also curve anterolaterally while tapering gradually to a point. They are usually longer than the first radials and are typically curved dorsally to articulate with the otoglossal cartilage. In contrast to the first radials, the second radials do have muscles attached to them. This second pair was shown by Drüner (1901) to arise at metamorphosis. He showed in *Salamandra* that the second pair of radials forms while the first pair is still present. Later, while investigating *Triturus*, Bogoljubsky (1924) also found a second pair of radials forming while the first pair was still in place. The first pair was later lost, and only the second pair was found to be present in the fully transformed adult. Özeti and Wake (1969) found several genera of salamandrids *Chioglossa*, *Salamandrina*, *Taricha*, *Triturus*, *Notophthalmus*, *Cynops*, and *Paramesotriton*) to have only one pair of radials in the adults, and, moreover, there were muscles attached to this pair. In those salamanders which have two pairs of radials, it seems likely that the second pair is homologous with the single pair of other genera.

Özeti and Wake (1969) report an "interradial cartilage" extending between the two second radials, and a structure by the same name had been reported earlier by others (Drüner, 1901; Kallius, 1901; Stadtmüller, 1936). Oppel (1900) found a ligamentous plate, the "sehnenplatte," in the substance of the tongue in *Salamandra maculosa* which serves for the attachment of the hyoglossus muscle and also for the insertion of the abdominohyoideus (rectus cervicis profundus). One of the morphological characters that has been used to distinguish primitive salamanders is the otoglossal cartilage (Dunn, 1926). Cope (1887) figured the otoglossal cartilage in his drawings of the hyobranchial skeleton of ambystomids and shows this structure forming an arc between the tips of the second radials. We likewise have found this structure in the specimens which were dissected. It is a semicircular ring of cartilage, the ends of which are attached to the tips of the second radials with the arch directed dorsad into the substance of the tongue. In some species, it may be jointed at the midline. It serves as an attachment for the rectus cervicis profundus and genioglossus muscles. It is hinged at its junction with the 2nd radial and apparently rotates forward with the radial cartilages as the tongue is extended in feeding. Tanner (1952) indicated that the "lingual cartilage" was missing in all of the Plethodontidae which he studied, and Dunn (1926) states that it is missing in all Plethodontidae, although Piatt (1935) reported finding it in several plethodontids. We believe that the interradial cartilage referred to above is in reality the otoglossal cartilage and that the "sehnenplatte" or "lingual cartilage" is a vestige of this structure as it exists in salamanders in which the tongue has attained a greater degree of freedom from the floor of the mouth than that which is seen in the Ambystomidae. Its position dorsal to the first basibranchial, its attachment to the second radial cartilages, and the fact that the rectus cervicus profundus also inserts on this structure in some of the Salamandridae seem to confirm such a belief.

The first branchial arch is formed by a narrow, curved bar of cartilage consisting of the first ceratobranchial and the epibranchial. The proximal end of the first ceratobranchial attaches to the posterolateral edge of the first basibranchial and extends posterolaterally and also somewhat dorsally, such that the posterior portion lies parallel with the ceratohyal. It is a flat oval in cross section and is wholly cartilaginous in the ambystomids observed, with the exception of one specimen in which a small ossification center was found (Table 1). Others (Hilton, 1947b; Özeti and Wake, 1969), in working with the salamandrids, have found this element to be well

Fig. 1. *Dicamptodon ensatus*. Upper left: Superficial throat musculature. Upper right: Intermediate muscles of the throat. Lower left: Deep muscles of the throat. Lower right: Hyobranchial skeleton.

al, aponeurosis lingualis; bI, first basibranchial; bII, second basibranchial; cI, first ceratobranchial; cII, second ceratobranchial; ch, ceratohyal; eb, epibranchial; gd, dorsal genioglossus; gh, geniohyoideus; gv, ventral genioglossus; hb, hebosteoypsiloideus; hy hyoglossus; ih, interhyoideus posterior; ip, intermandibularis posterior; iq, interossaquadrata; la, linea alba; m, mandible; og, otoglossal; ogp, otoglossal plate; oh, omohyoideus; p, pectoralis; pc, pericardium; rI, first radial; rII, second radial, rp, rectus cervicis profundus; rs, rectus cervicis superficialis; s, sternum; sh, subhyoideus; sr, subarcualis rectus I, t tendon.

Fig. 2. *Rhyacotriton olympicus.* Upper left: Superficial throat musculature. Upper right: Intermediate muscles of the throat. Lower left: Deep muscles of the throat. Lower right: Hyobranchial skeleton.

Fig. 3. *Ambystoma annulatum.* Upper left: Superficial throat musculature. Upper right: Intermediate muscles of the throat. Lower left: Deep muscles of the throat. Lower right: Hyobranchial skeleton.

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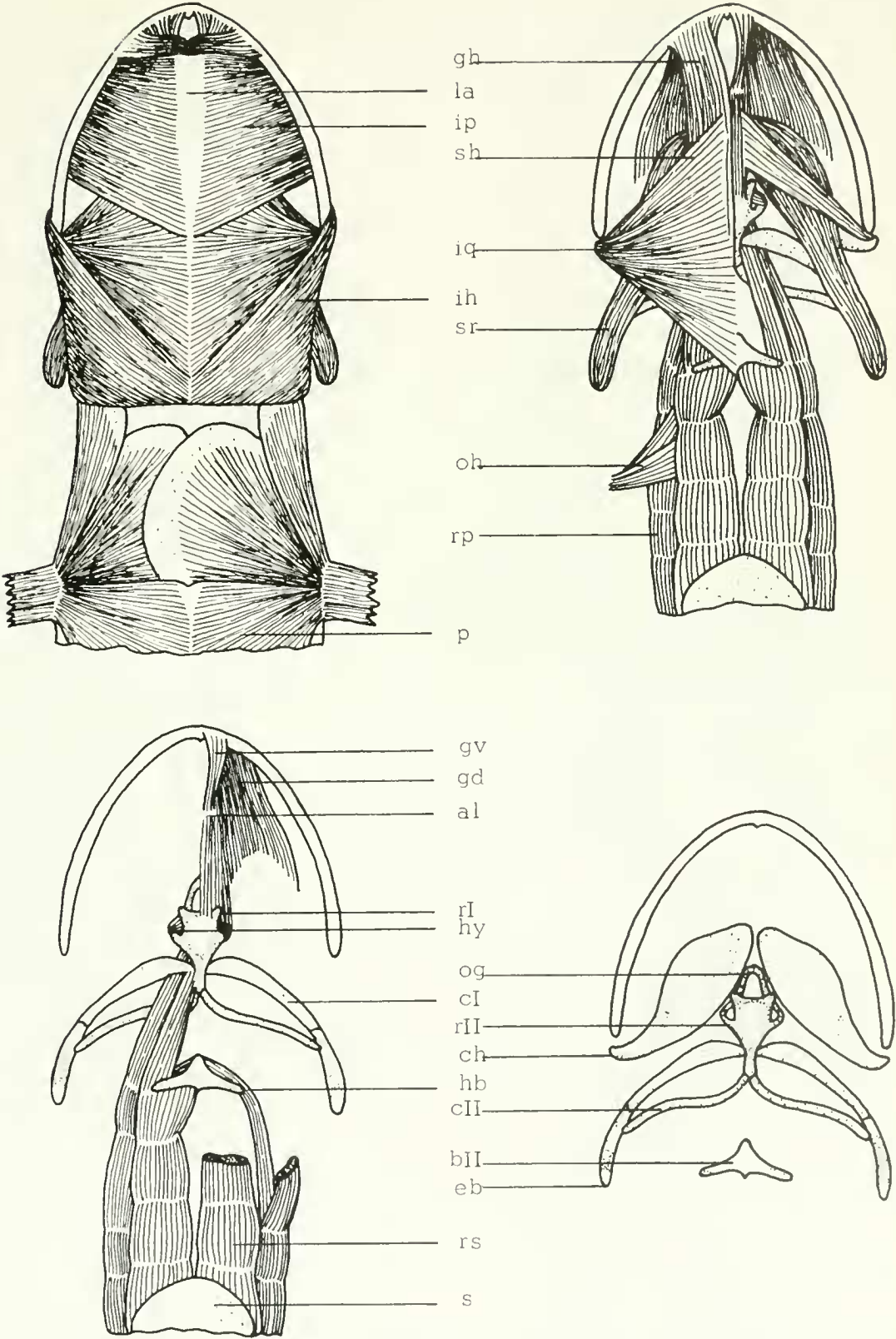
Fig. 4. *Ambystoma cingulatum.* Upper left: Superficial throat musculature. Upper right: Intermediate muscles the throat. Lower left: Deep muscles of the throat. Lower right: Hyobranchial skeleton.
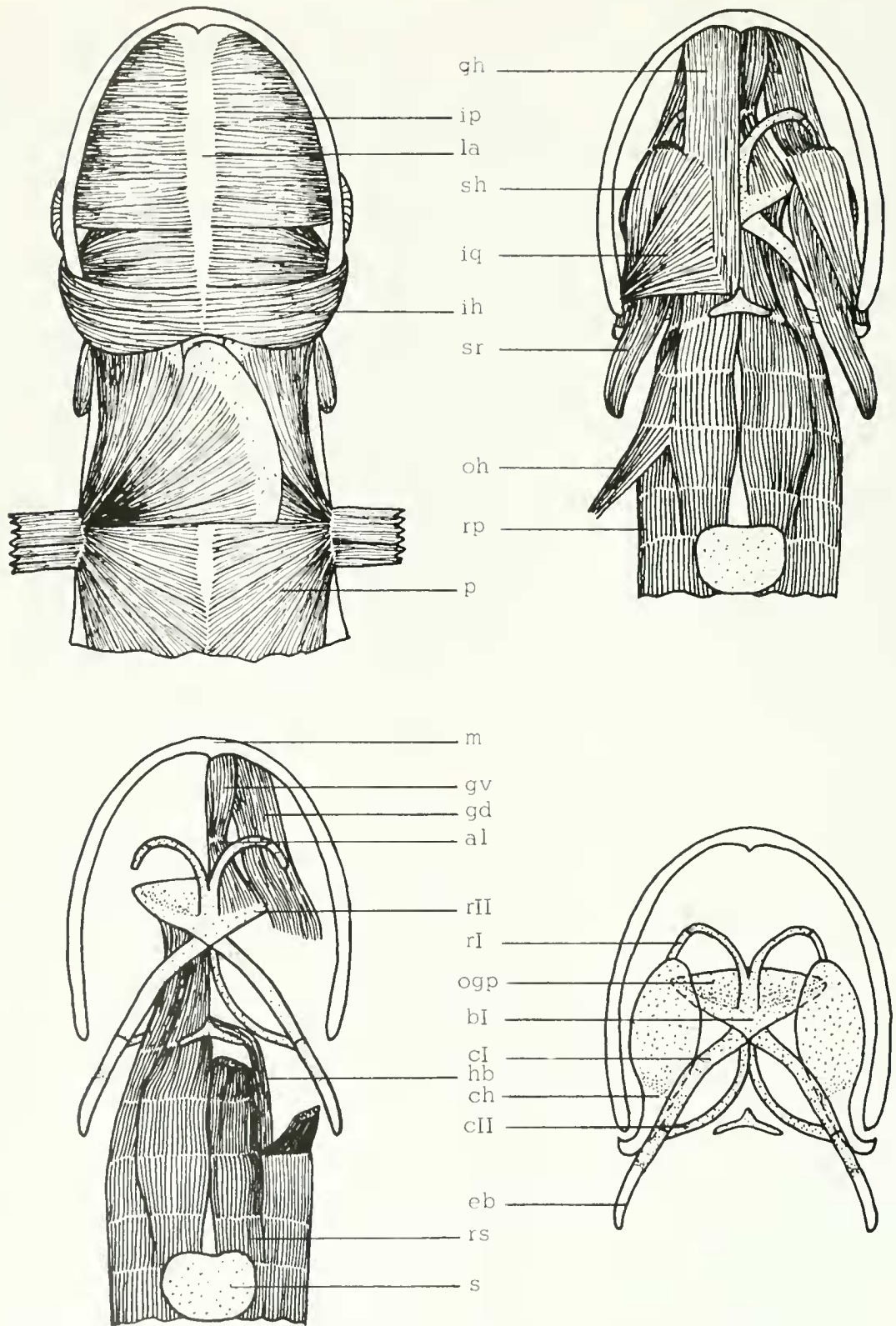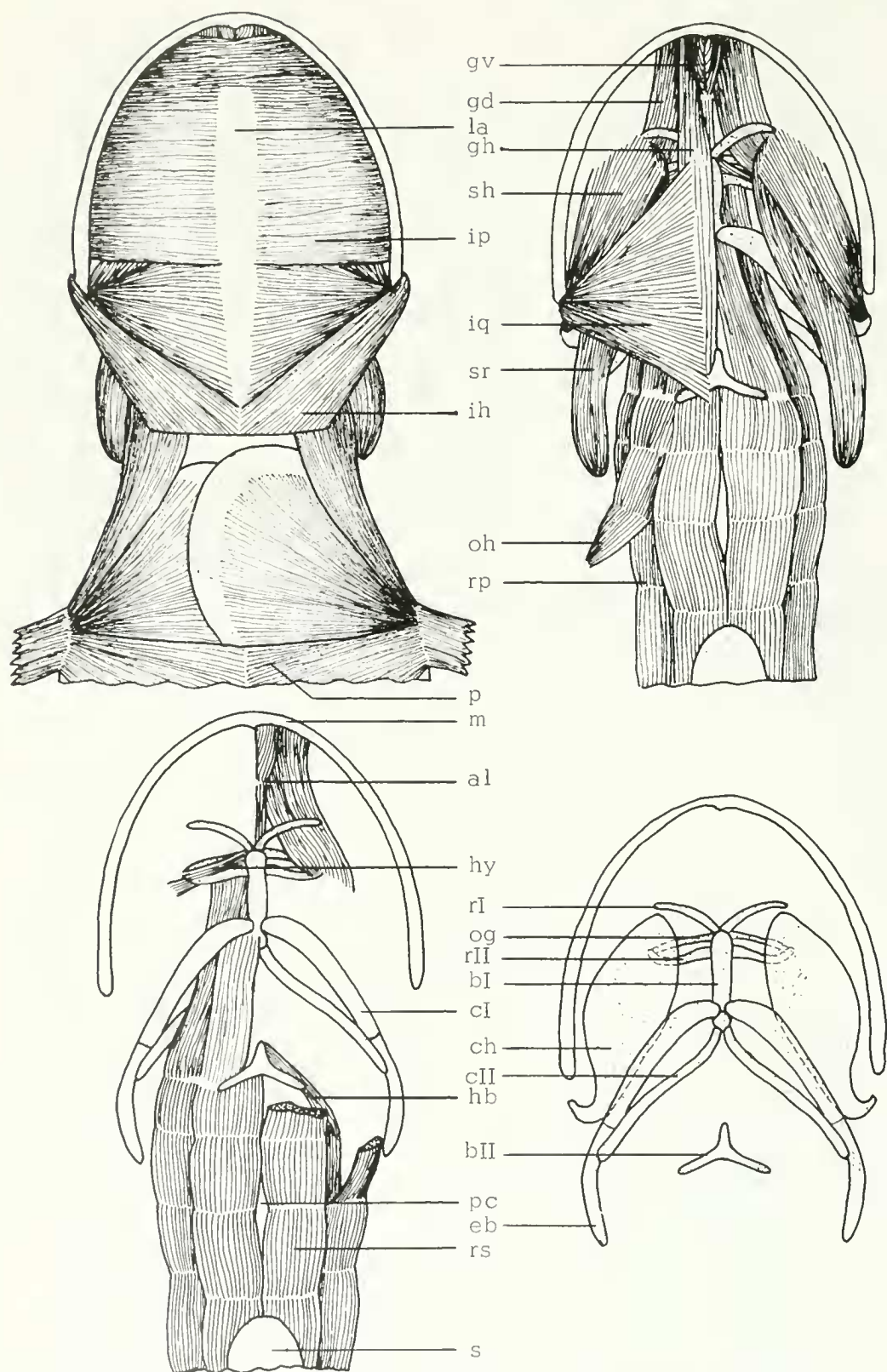
Fig. 5. *Ambystoma gracile.* Upper left: Superficial throat musculature. Upper right: Intermediate muscles of the throat. Lower left: Deep muscles of the throat. Lower left: Deep muscles of the throat. Lower right: Hyobranchial skeleton.
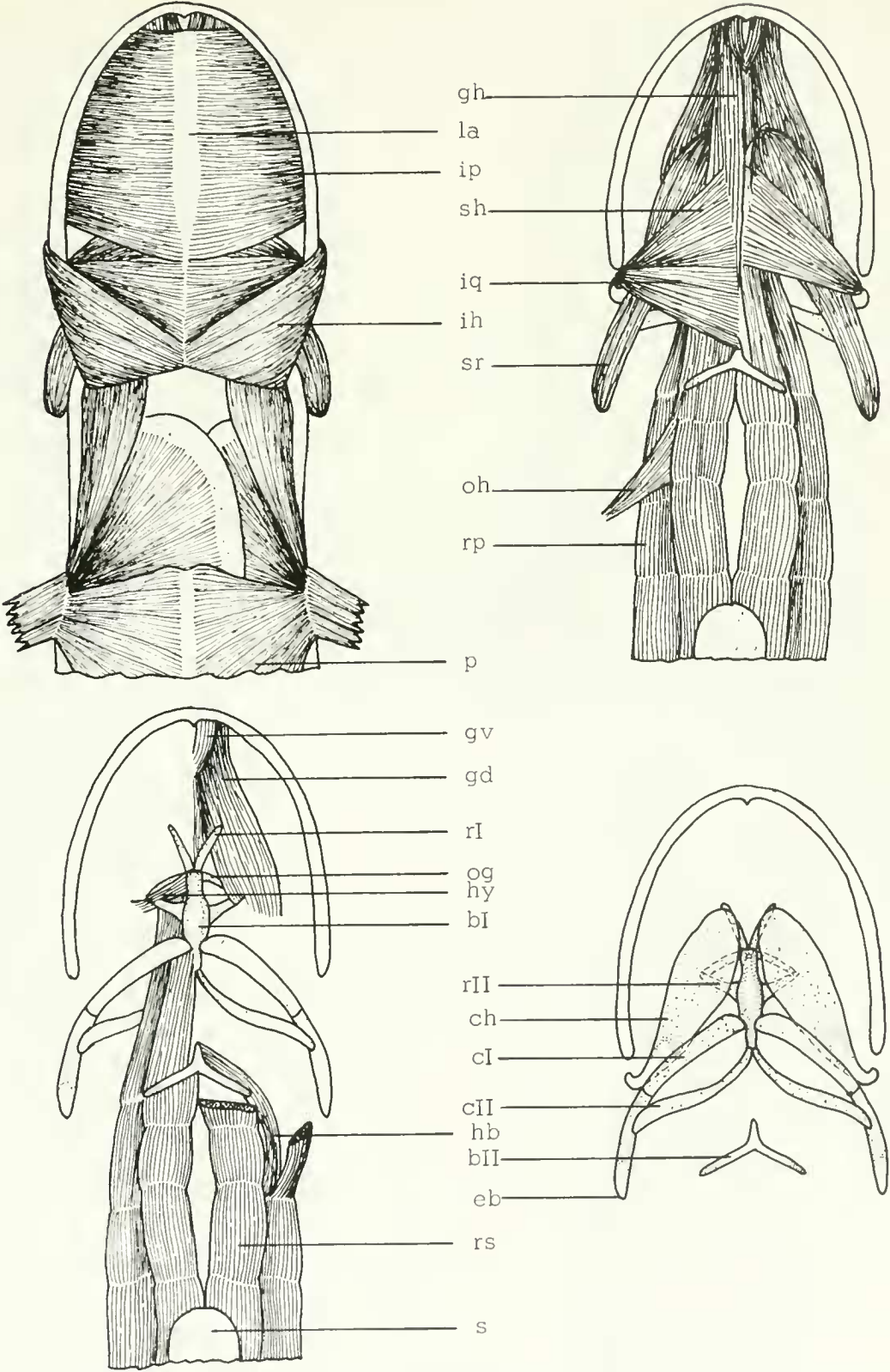
Fig. 6. *Ambystoma jeffersonianum*. Upper left: Superficial throat musculature. Upper right: Intermediate muscles of the throat. Lower left: Deep muscles of the throat. Lower right: Hyobranchial skeleton.
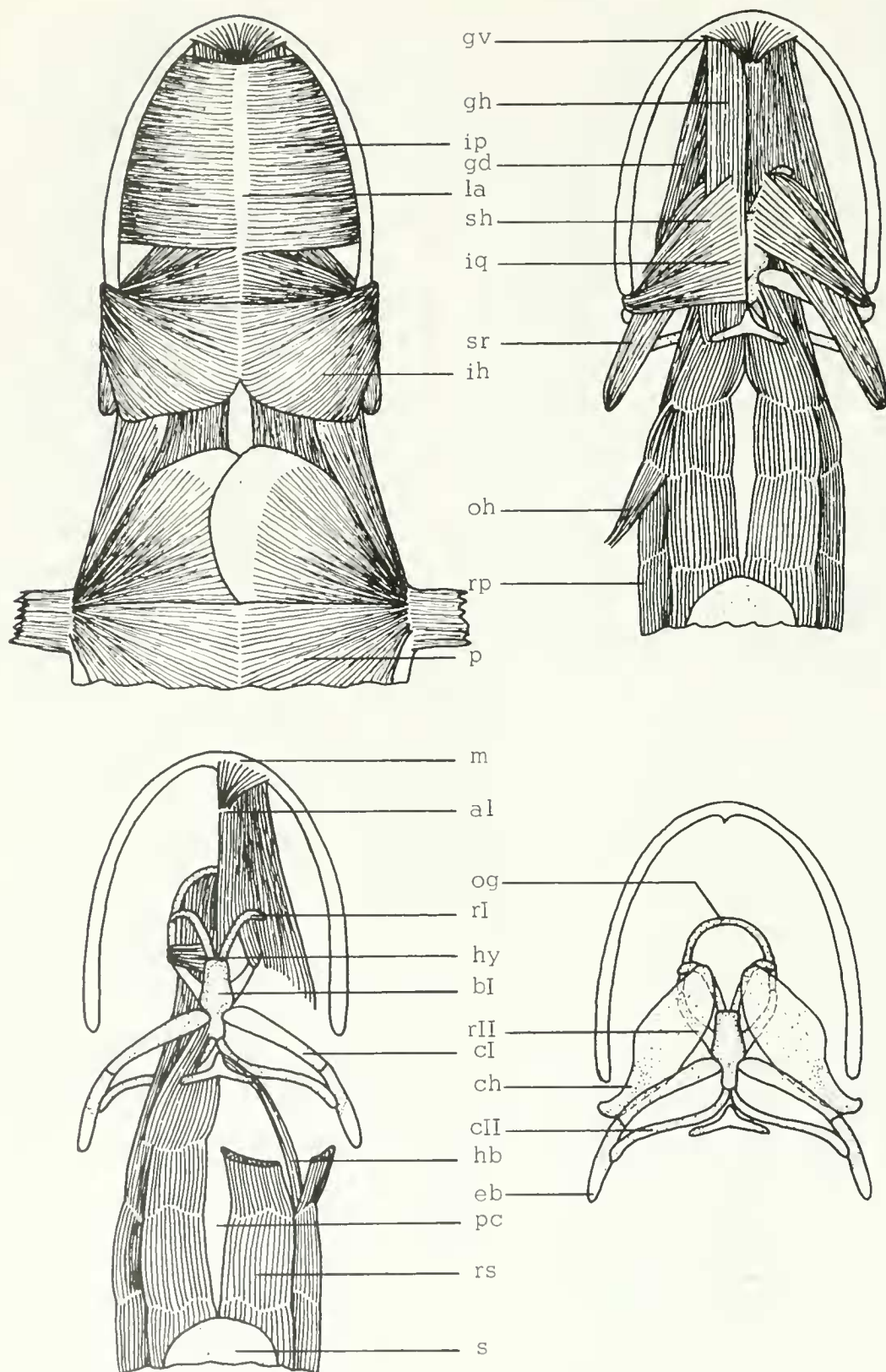
Fig. 7. *Ambystoma mabeei.* Upper left: Superficial throat musculature. Upper right: Intermediate muscles of the throat. Lower left: Deep muscles of the throat. Lower right: Hyobranchial skeleton.
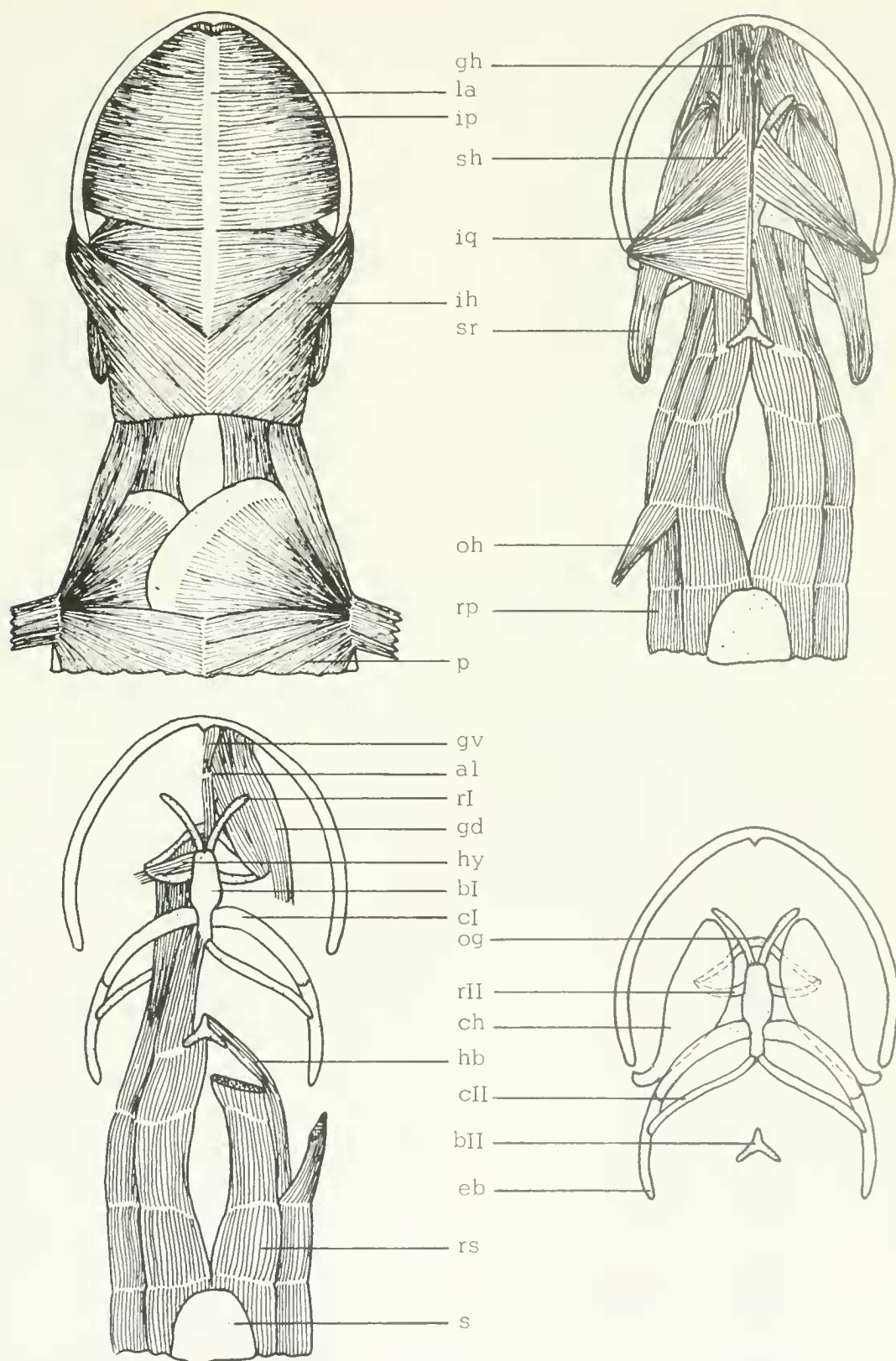
Fig. 8. *Ambystoma macrodactylum.*   Upper left: Superficial throat musculature. Upper right: Intermediate muscles of the throat. Lower left: Deep muscles of the throat. Lower right: Hyobranchial skeleton.
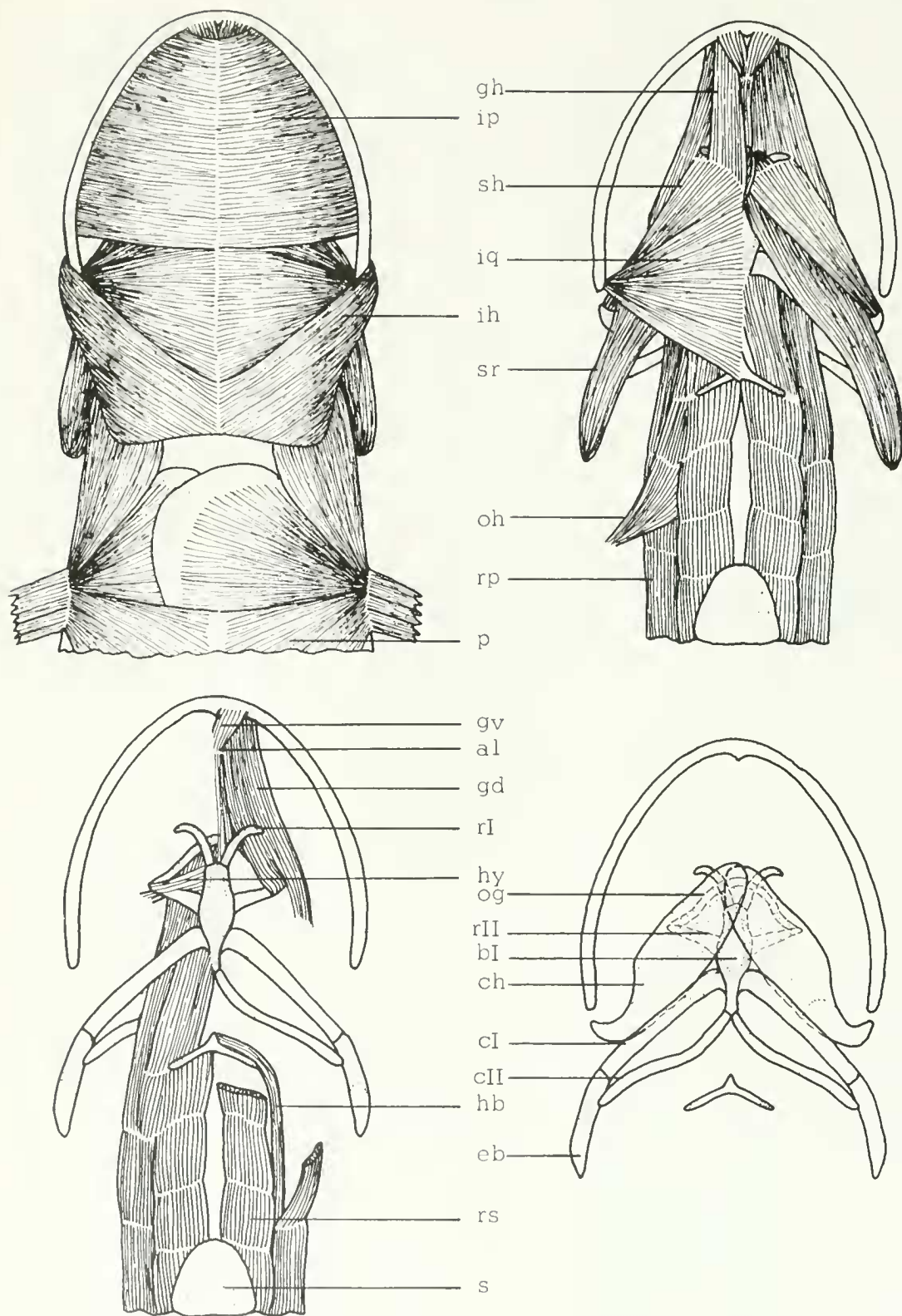
Fig. 9.   *Ambystoma maculatum*. Upper left: Superficial throat musculature. Upper right: Intermediate muscles of the throat. Lower left: Deep muscles of the throat. Lower right: Hyobranchial skeleton.

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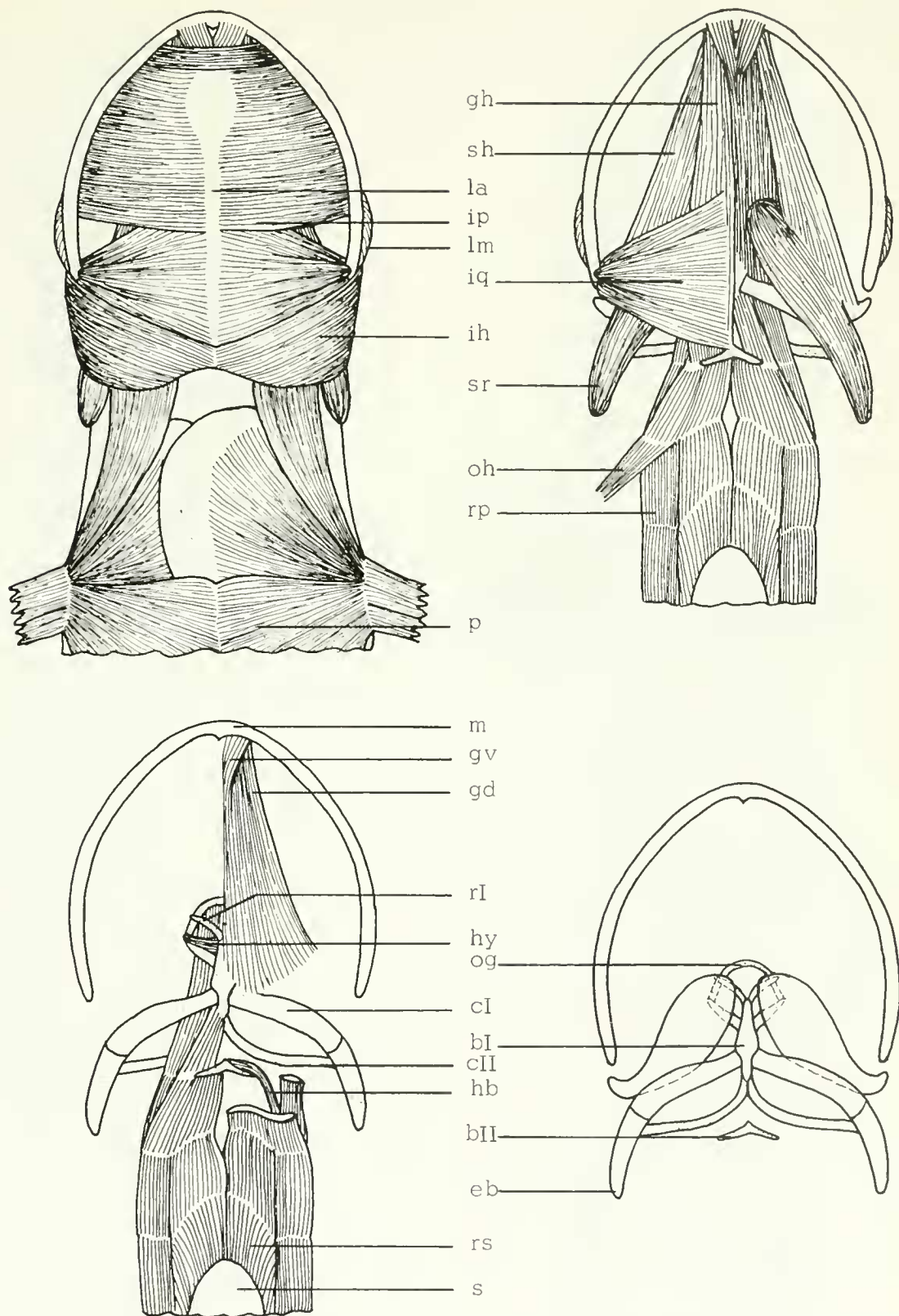oh
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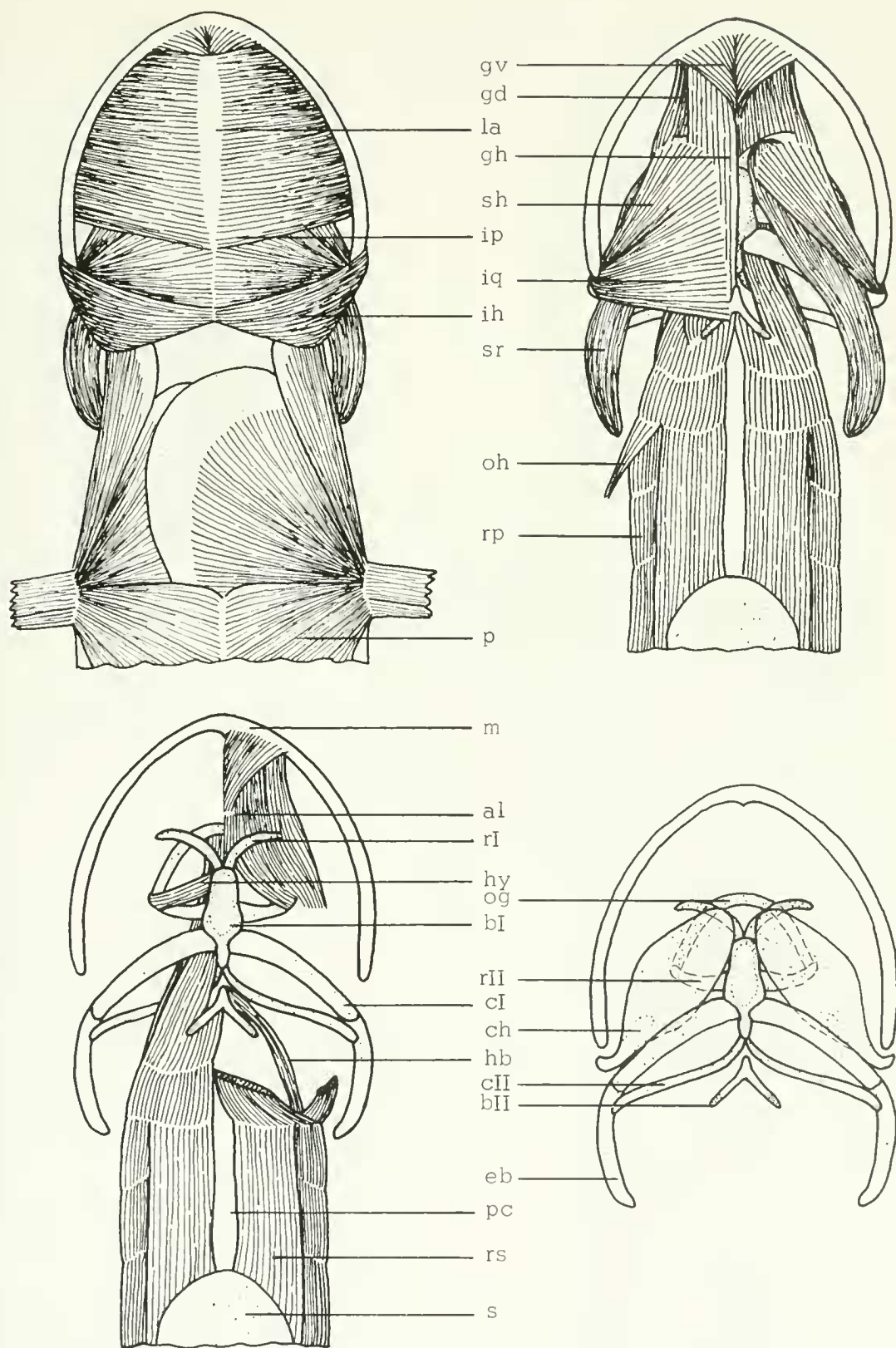
Fig. 10. *Ambystoma talpoideum.* Upper left: Superficial throat musculature. Upper right: Intermediate muscles of the throat. Lower left: Deep muscles of the throat. Lower right: Hyobranchial skeleton.
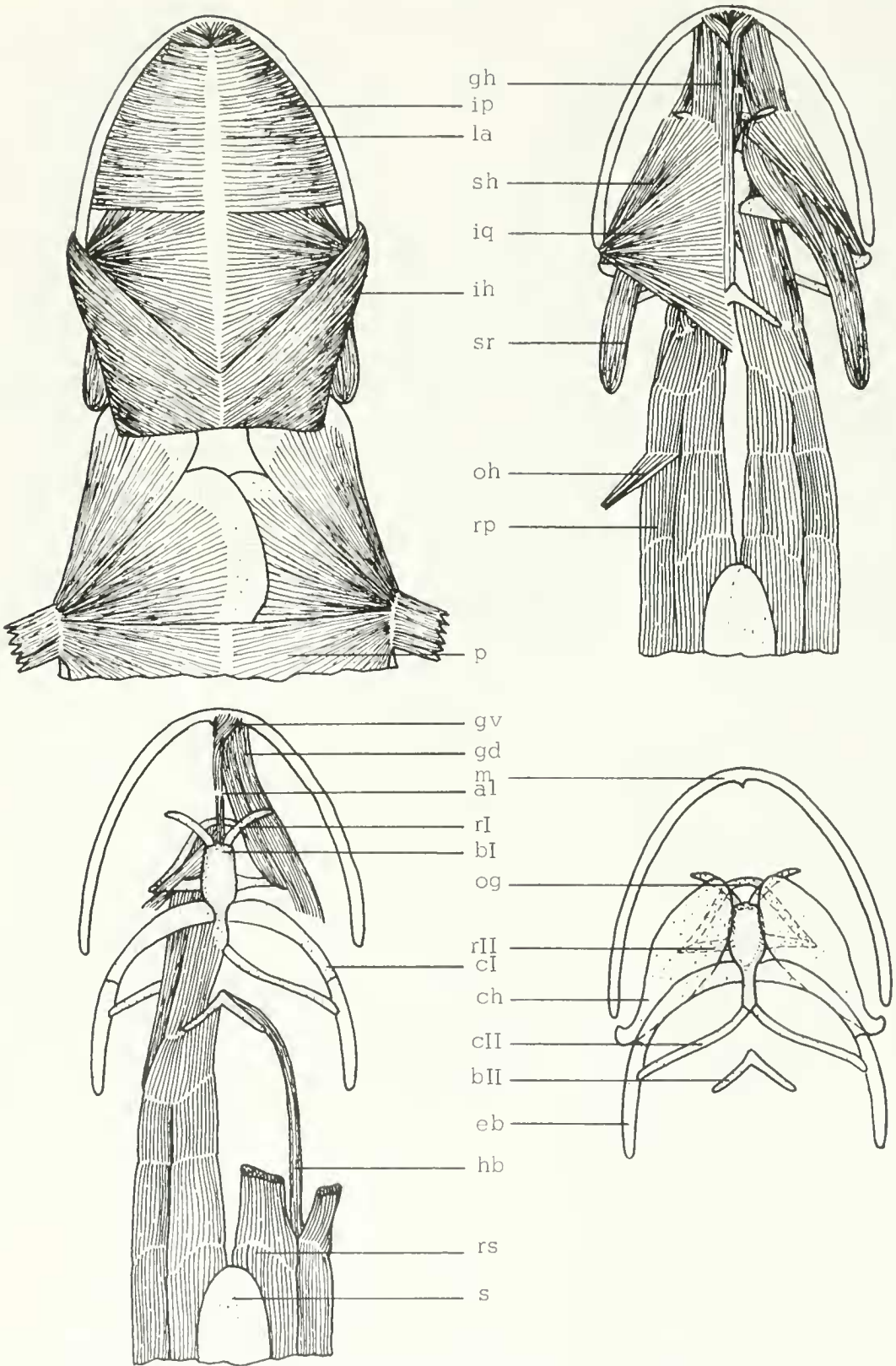
Fig. 11. *Ambystoma opacum.* Upper left: Superficial throat musculature. Upper right: Intermediate muscles of the throat. Lower left: Deep muscles of the throat. Lower right: Hyobranchial skeleton.
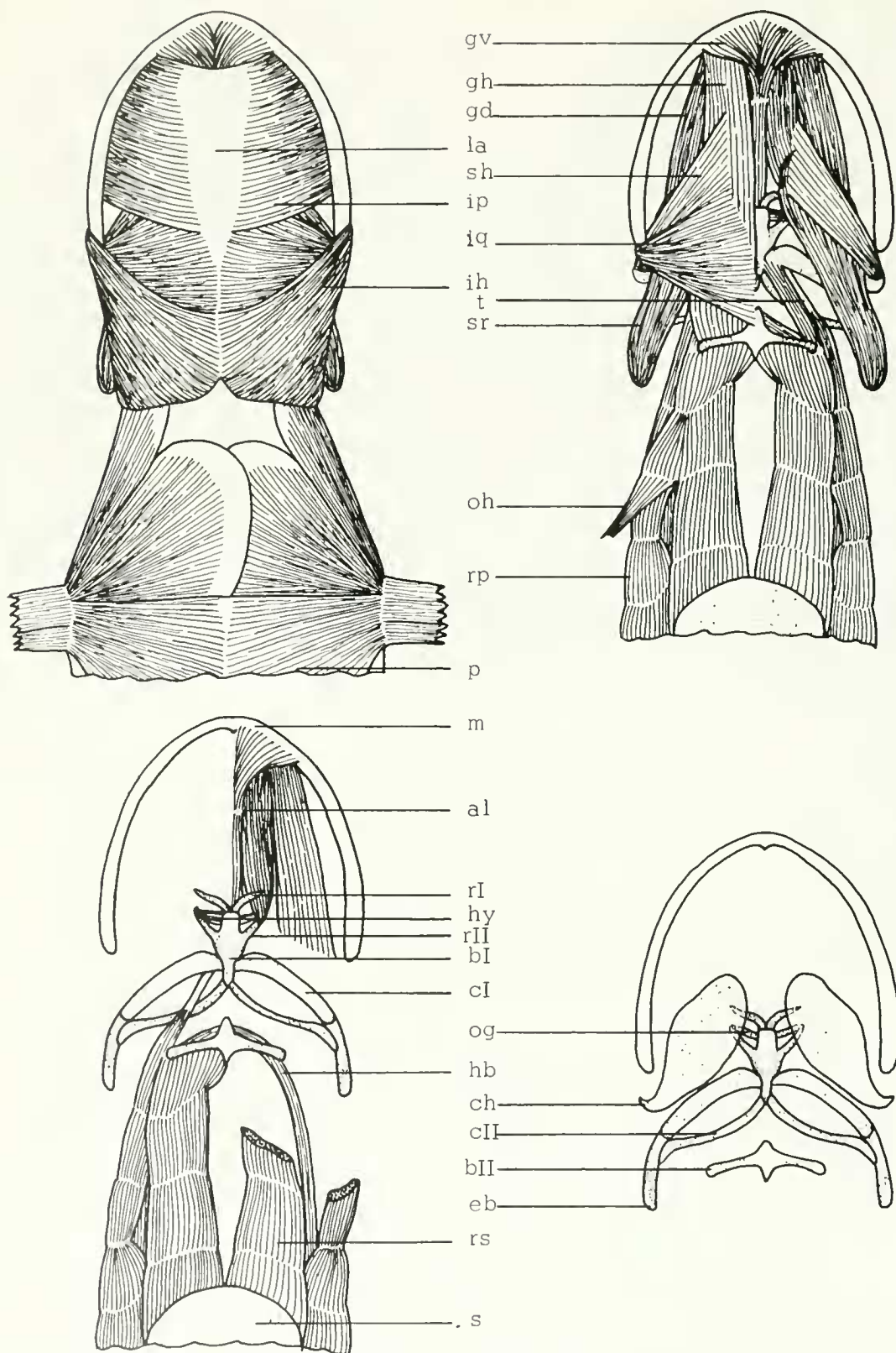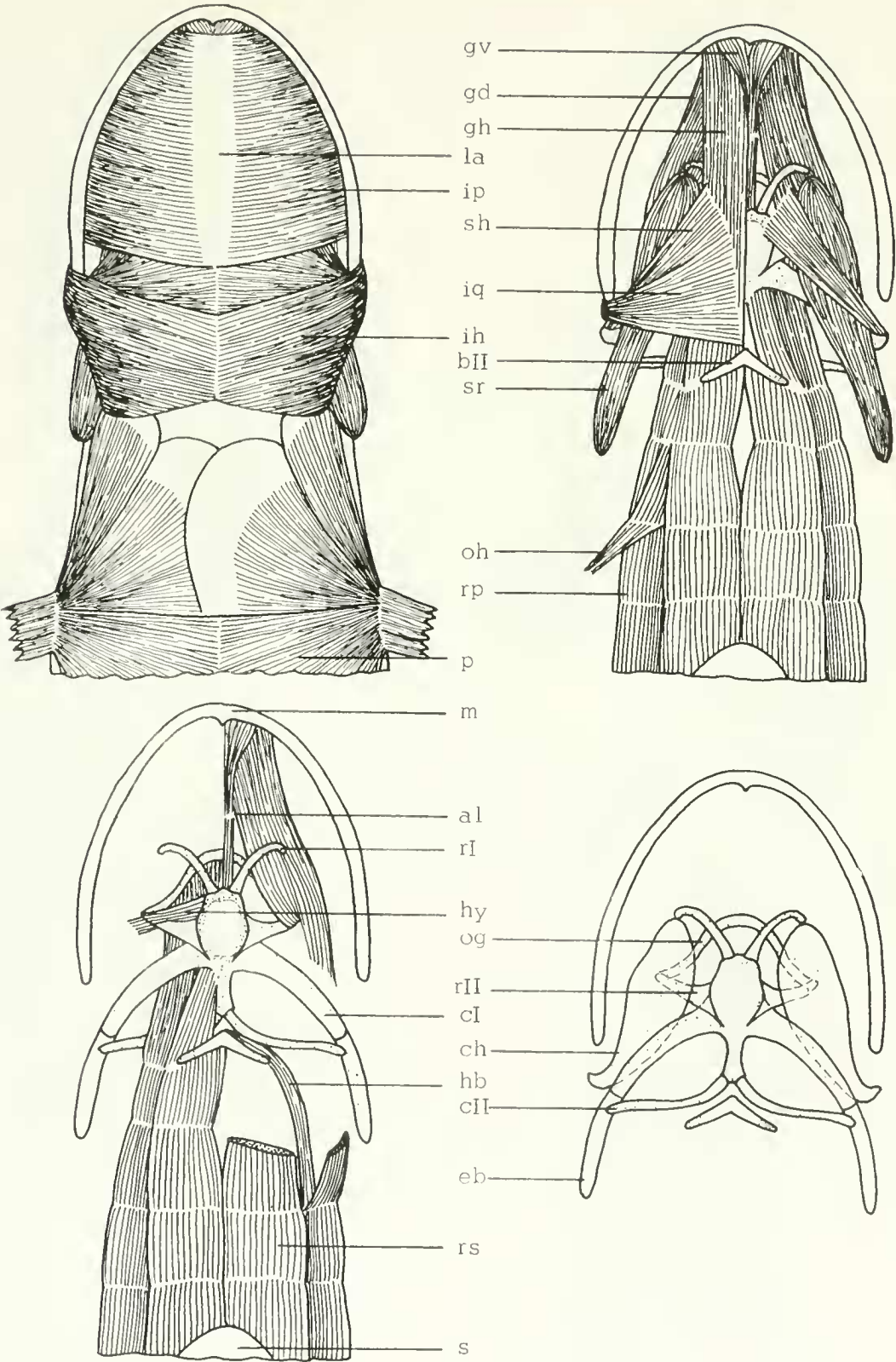
Fig. 12. *Ambystoma texanum.* Upper left: Superficial throat musculature. Upper right: Intermediate muscles of the throat. Lower left: Deep muscles of the throat. Lower right: Hyobranchial skeleton.
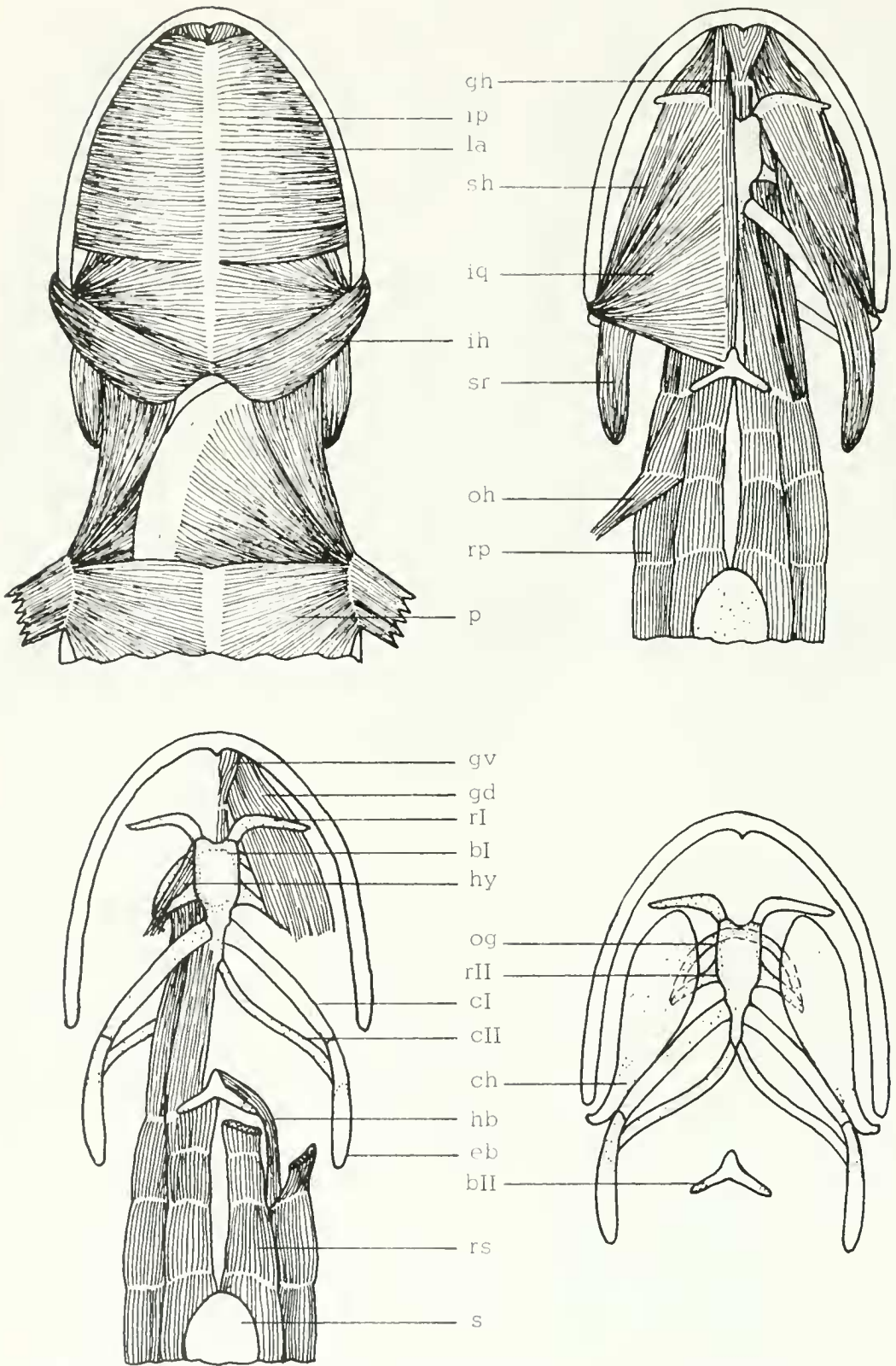
Fig. 13. *Ambystoma rosaceum*. Upper left: Superficial throat musculature. Upper right: Intermediate muscles of the throat. Lower left: Deep muscles of the throat. Lower right: Hyobranchial skeleton.

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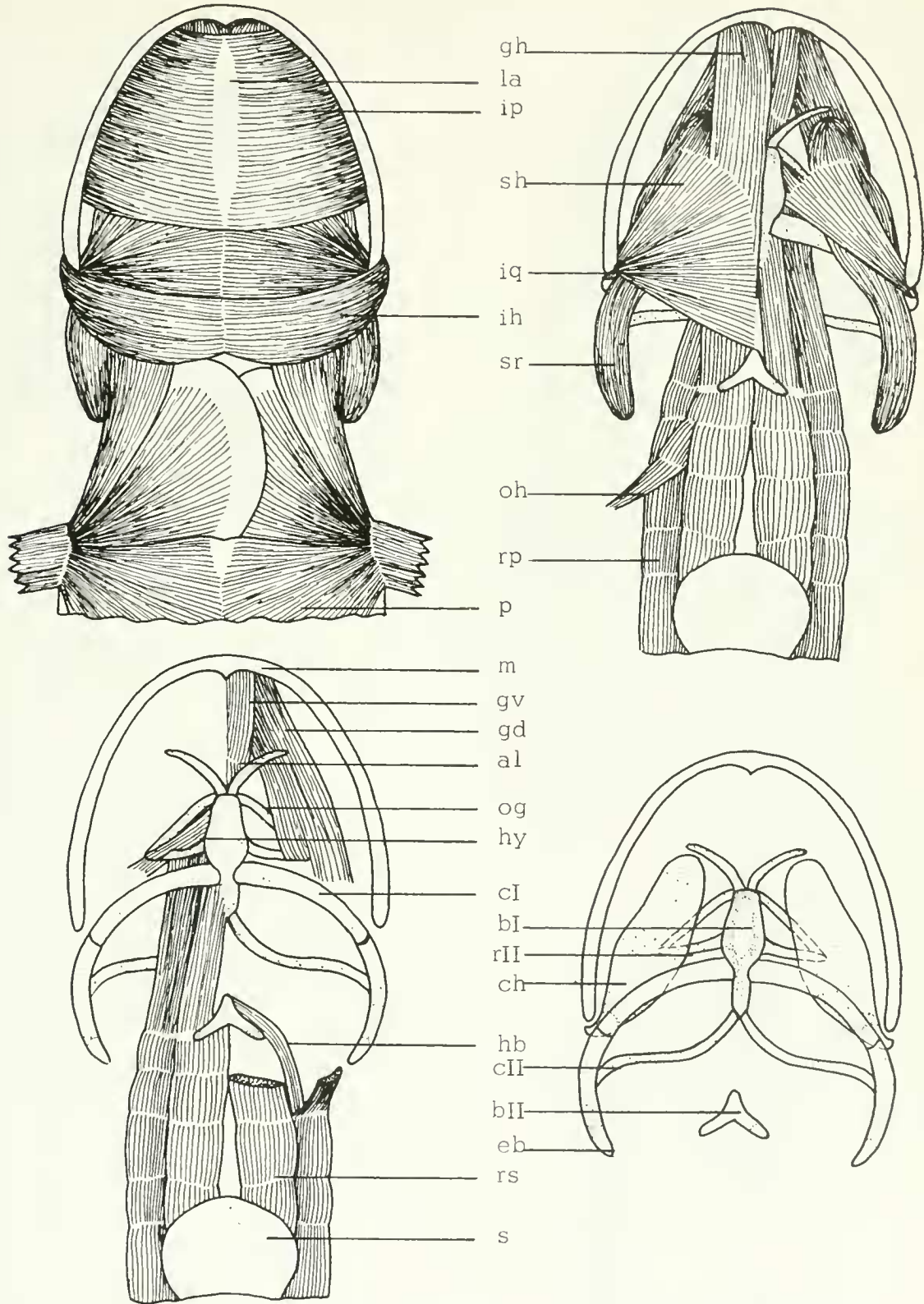
Fig. 14.   *Ambystoma tigrinum*. Upper left: Superficial throat musculature. Upper right: Intermediate muscles of the throat. Lower left: Deep muscles of the throat. Lower right: Hyobranchial skeleton.
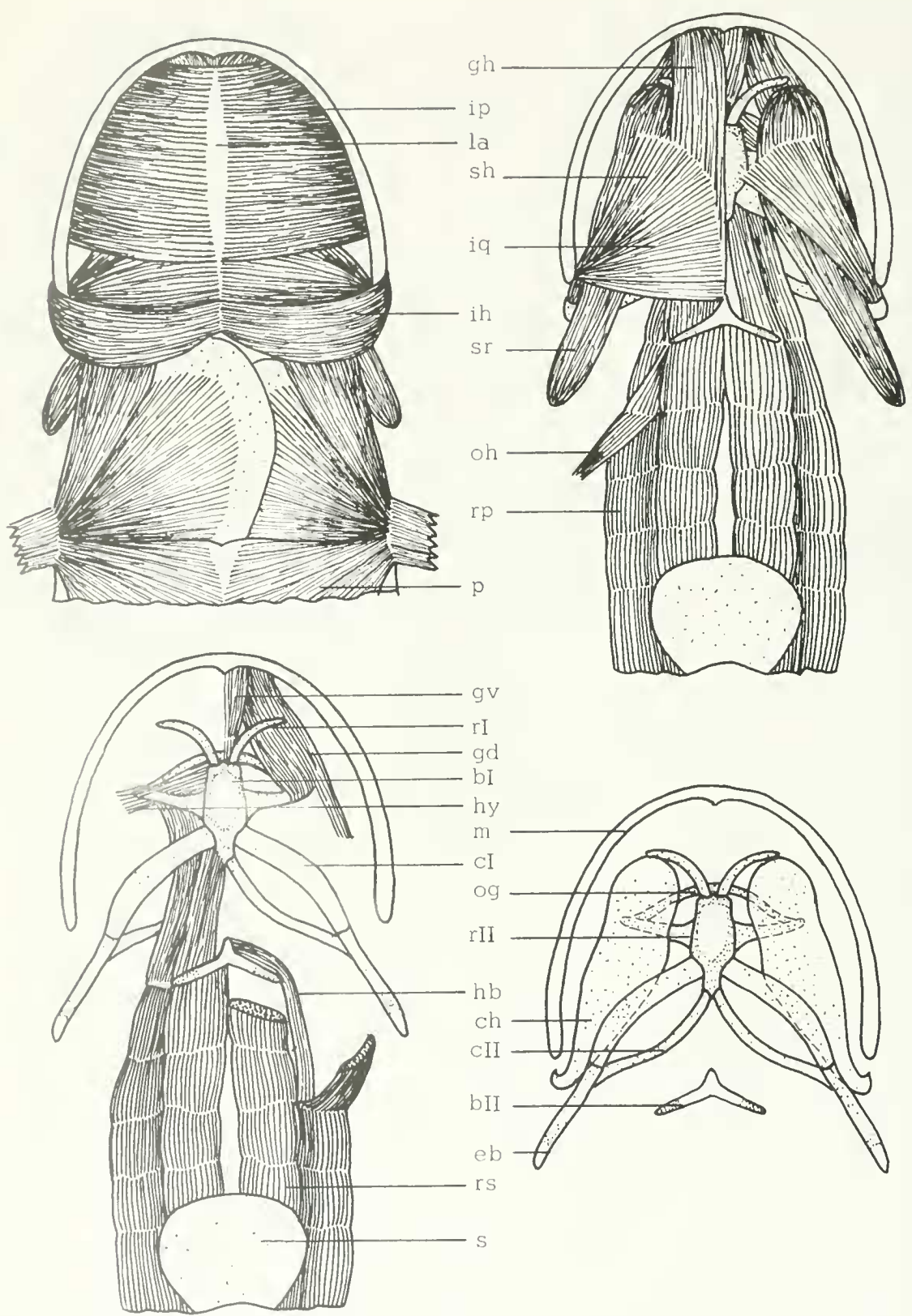
Fig. 15. *Ambystoma tigrinum melanostictum*. Upper left: Superficial throat musculature. Upper right: Intermediate muscles of the throat. Lower left: Deep muscles of the throat. Lower right: Hyobranchial skeleton.

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og
rII
ch
cI
cII
hb
bII
eb
rs
s
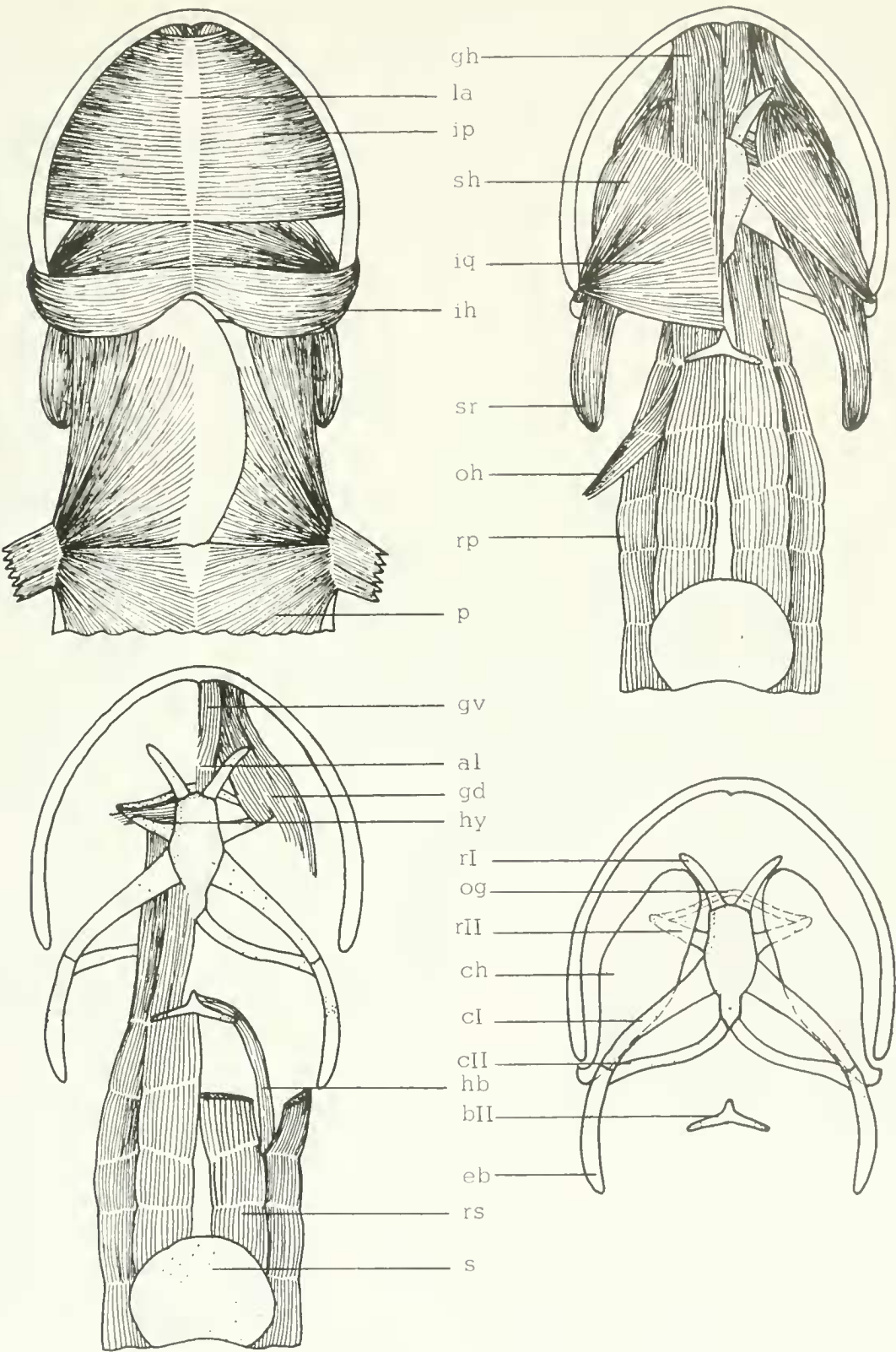
Fig. 16. *Ambystoma tigrinum nebulosum.* Upper left: Superficial throat musculature. Upper right: Intermediate muscles of the throat. Lower left: Deep muscles of the throat. Lower right: Hyobranchial skeleton.
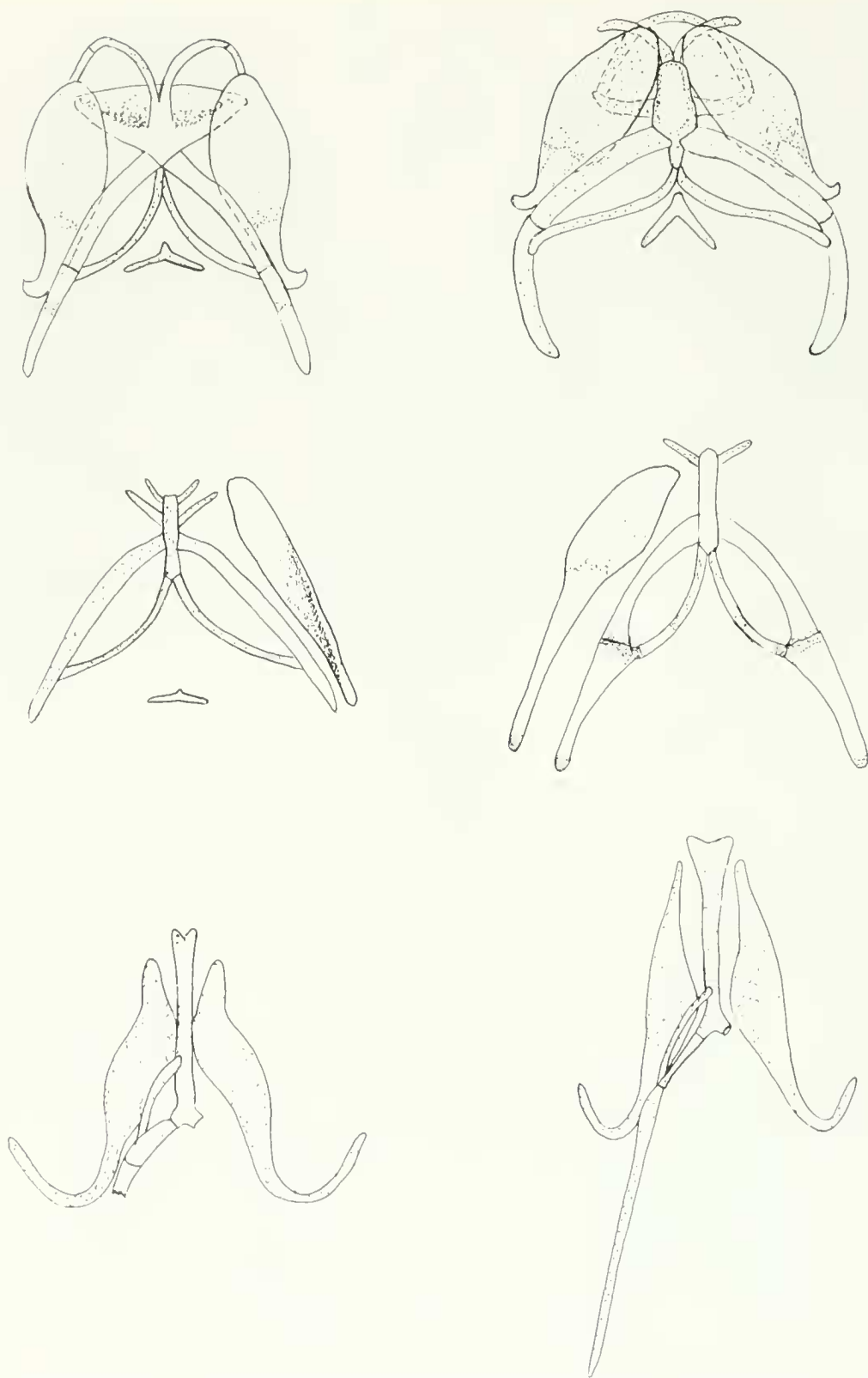
Fig. 17. Representative hyobranchial skeletons of Ambystomidae, Salamandridae, and Plethodontidae. Upper left: *Dicamptodon ensatus*. Upper right: *Ambystoma talpoideum*. Middle left: *Salamandra salamandra*. Middle right: *Taricha torosa*. Lower left: *Bolitoglossa rufescens*. Lower right: *Thorius narisovalis*. Middle left and middle right from Özeti and Wake (1969). Lower left and lower right from Tanner (1952).

ossified. The distal end of the first ceratobranchial attaches to the proximal end of the epibranchial, the articulation of which is usually perceptible only as a thin line separating these two elements. There is no second epibranchial. The posterior tip of the epibranchial is ossified in nine of the fourteen species which we have dissected and serves as an attachment for the subarcualis rectus 1 muscle. Özeti and Wake (1969) report that the epibranchial is usually almost entirely

Table 1. Average percent ossification of hyobranchial elements.

Species	bI	bII	cI	cII	rI	rII	ch	eb
Dicamptodon ensatus	0.0	0	0.0	0	0	0	15.0	56.5
Rhyacotriton olympicus	0.0	0	0.0	0	0	0	0.0	0.0
Ambystoma annulatum	77.0	43	0.0	0	0	0	0.0	12.0
Ambystoma cingulatum	73.0	62	2.2	0	0	0	5.0	15.0
Ambystoma gracile	0.0	78	0.0	0	0	0	0.0	0.0
Ambystoma jeffersonianum	37.4	80	0.0	0	0	0	6.4	39.7
Ambystoma mabeei	37.0	63	0.0	0	0	0	6.8	58.0
Ambystoma macrodactylum	34.0	50	0.0	0	0	0	5.0	0.0
Ambystoma maculatum	25.0	73	0.0	0	0	0	10.6	32.0
Ambystoma talpoidcum	32.6	76	0.0	0	0	0	3.6	0.0
Ambystoma opacum	41.0	0	0.0	0	0	0	2.7	11.0
Ambystoma texanum	38.0	65	0.0	0	0	0	3.3	0.0
Ambystoma rosaceum	28.0	69	0.0	0	0	0	4.8	36.0
Ambystoma tigrinum	40.0	72	0.0	0	0	0	5.0	17.0
Ambystoma tigrinum melanostictum	37.5	71	0.0	0	0	0	0.0	21.0
Ambystoma tigrinum nebulosum	59.0	59	0.0	0	0	0	8.0	60.0

ossified in the Salamandridae but that some genera have lost this element or have experienced a fusion of the latter with the ceratobranchial. These investigators also report that the epibranchial is longer than the ceratobranchial, but we have found that the ambystomid epibranchial is consistently shorter than the first ceratobranchial with which it is articulated (Table 13).

The second branchial arch consists of a pair of slender, curved bars of cartilage which articulate proximally with the posterior end of the first basibranchial and curve posterolaterally to articulate distally with the first branchial arch at a point about two-thirds along the latter's length. It is entirely cartilaginous in all specimens which we have observed. The space between these two arches is covered by the intercartilaginous membrane (Drüner, 1901) except for the mesial portion through which the rectus cervicis profundus passes.

The second basibranchial is a small element located in the tendonous inscription which separates the geniohyoideus from the rectus cervicis superficialis. It usually assumes the shape of a three-pointed star in which one arm is directed anteriorly with the other two arms pointing posterolaterally. In most of the specimens studied in this paper, the second basibranchial is cartilaginous on the tips of the lateral arms, the remainder being ossified. In a few specimens, the entire element is cartilage. In the larval state, this structure is connected with the first basibranchial by a slender median rod which disappears at metamorphosis, leaving the two basibranchials separated from each other. In most genera of the Salamandridae, the second basibranchial is lost (Özeti and Wake, 1969), and in the Plethodontidae it is reported by some authorities as completely missing (Dunn, 1926; Tanner, 1952; Wake, 1966), although Piatt (1935) recorded its presence in several plethodontid genera.

GENERAL FEATURES OF THE MUSCULATURE

The following paragraphs constitute some general statements as to position and size of the throat muscles. More detailed descriptions will be found in the following section which deals with each species.

Intermandibularis Posterior

This muscle is found just under the skin of the throat and covers about two-thirds of the area between the two rami of the mandible. There are two intermandibularis muscles in the larva, a small anterior portion, and a larger posterior portion. It is the posterior portion that persists in the adult, and the anterior portion, the intermandibularis anterior, is lost at the time of transformation, or if it persists it is so completely fused with the posterior muscle that no separation can be made in adults. The origin of the intermandibularis posterior is along the dorsomedial surface of the mandible. In most specimens there is a small open area at the angle of

the chin where there are no fibers and the ventral portion of the genioglossus can be seen upon removal of the skin. The insertion is at the midline fascia of the throat—the linea alba. The width of this fascia is variable among the several species studied. In *Rhyacotriton* and *A. gracile* the fibers of the anterior portion extend without interruption across the midventral line. Also, in *A. cingulatum* the anterior portion of the intermandibularis posterior is noticeably separate from the large posterior portion of the muscle. The anterior portion of the interossaquadrata is covered ventrally by the posterior fibers of this muscle.

This is one of the least variable muscles of the throat area. Contraction results in the raising of the floor of the mouth, which is a component of the breathing mechanism. This action also helps to force food items up against the vomerine teeth in feeding.

Interhyoideus Posterior

It has been suggested (Piatt, 1940) that this muscle in the Plethodontidae gives rise to two adult muscles, the gularis and the quadratopectoralis. In the ambystomids we have seen no tendency toward subdivision of the interhyoideus posterior, and it would therefore appear that this muscle is undifferentiated as noted by Piatt (1940). The origin is in fascia which attaches to the tip of the mandible, the quadrate, the squamosal, and the otic capsule and is continuous with the fascia cephalodorsalis. The fibers extend ventromesial to insert into the skin of the gular fold and the fascia along the midventral line.

This muscle would appear to function in swallowing food and in breathing, inasmuch as it is in a position to constrict the pharynx. It might also act in head flexion, since the posterior fibers are attached to the skin of the gular fold.

Table 2. Numeric Characters[1]

Species	Museum Number	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
Dicamptodon	32467	0.50	0.75	1.29	0.52	0.21	0.55	0.27	0.47	2.09	0.52	0.93	1.10	0.53	0.55	0.35	0.72	0.36	00.0	00.0	00.0	16.0	60.0
Dicamptodon	32465	0.49	0.71	1.09	0.55	0.21	0.45	0.25	0.40	1.90	0.55	1.21	0.91	0.50	0.53	0.29	0.71	0.39	00.0	00.0	00.0	14.0	53.0
Rhyacotriton	12480	0.40	0.64	1.03	0.80	0.27	0.50	0.29	0.27	1.07	0.54	1.15	1.17	0.63	0.35	0.18	0.91	0.37	00.0	00.0	00.0	00.0	0.00
Rhyacotriton	12479	0.35	0.62	0.97	0.89	0.33	0.38	0.21	0.33	1.20	0.56	1.26	0.85	0.47	0.29	0.31	1.16	0.31	00.0	00.0	00.0	0.00	0.00
A. annulatum	32521	0.38	0.67	1.02	0.83	0.23	0.46	0.27	0.43	0.62	0.60	1.48	1.15	0.69	0.39	0.29	0.73	0.39	73.0	48.0	00.0	00.0	20.0
A. annulatum	32522	0.37	0.67	1.06	0.83	0.24	0.45	0.26	0.58	0.71	0.58	1.39	1.08	0.63	0.40	0.40	0.72	0.38	78.0	54.0	00.0	00.0	07.0
A. annulatum	32523	0.36	0.66	1.10	0.91	0.21	0.48	0.25	0.55	0.55	0.53	1.14	1.33	0.71	0.41	0.43	0.67	0.37	84.0	42.0	00.0	00.0	07.0
A. annulatum	32524	0.39	0.67	1.09	0.97	0.21	0.41	0.26	0.71	0.81	0.63	1.70	1.25	0.79	0.41	0.24	0.71	0.39	75.0	32.0	00.0	00.0	10.0
A. annulatum	32525	0.39	0.63	1.03	1.05	0.24	0.49	0.27	0.59	0.77	0.54	1.18	1.22	0.66	0.37	0.35	0.71	0.35	78.0	12.0	00.0	00.0	16.0
A. cingulatum	33307	0.42	0.71	1.11	0.75	0.25	0.50	0.29	0.72	0.22	0.57	1.33	1.17	0.67	0.46	0.50	0.77	0.32	60.0	60.0	00.0	09.0	18.0
A. cingulatum	33309	0.14	0.75	1.13	0.71	0.23	0.43	0.26	0.93	0.33	0.61	1.59	1.20	0.74	0.45	0.48	0.82	34	72.0	52.0	00.0	00.0	28.0
A. cingulatum	33310	0.39	0.71	0.89	0.77	0.21	0.43	0.26	0.80	0.33	0.61	1.59	1.09	0.67	0.48	0.41	0.71	0.33	90.0	63.0	00.0	08.0	00.0
A. cingulatum	33312	0.47	0.69	1.14	0.86	0.21	0.45	0.31	0.73	0.27	0.67	2.06	1.12	0.76	0.50	0.41	0.77	0.35	78.0	71.0	00.0	00.0	00.0
A. cingulatum	33308	0.40	0.67	1.03	0.82	0.21	0.46	0.28	0.69	0.38	0.60	1.52	1.17	0.71	0.48	0.58	0.66	0.37	67.0	11.0	18.0	08.0	27.0
A. gracile	32503	0.39	0.67	0.94	0.46	0.23	0.49	0.27	0.34	0.92	0.55	1.24	1.11	0.61	0.57	0.35	0.67	0.35	00.0	82.0	00.0	00.0	00.0
A. gracile	32504	0.38	0.69	0.99	0.55	0.24	0.55	0.27	0.46	0.86	0.50	1.00	1.14	0.57	0.49	0.45	0.78	0.32	00.0	74.0	00.0	00.0	00.0
A. jeffersonianum	32487	0.46	0.64	1.12	0.42	0.26	0.62	0.32	0.51	0.63	0.52	1.09	1.18	0.61	0.49	0.30	0.64	0.32	36.0	91.0	00.0	08.5	27.5
A. jeffersonianum	32489	0.44	0.68	1.00	0.44	0.25	0.61	0.31	0.46	0.66	0.50	1.00	1.12	0.56	0.52	0.55	0.69	0.26	34.5	85.0	00.0	06.1	32.0
A. jeffersonianum	32488	0.47	0.64	0.93	0.44	0.24	0.55	0.31	0.49	0.46	0.56	1.26	1.12	0.63	0.53	0.43	0.63	0.33	39.4	80.0	00.0	06.1	48.0
A. jeffersonianum	32508	0.49	0.70	1.12	0.42	0.25	0.57	0.31	0.41	0.68	0.55	1.20	1.12	0.61	0.53	0.45	0.69	0.28	39.0	82.0	00.0	05.9	45.0
A. jeffersonianum	32509	0.45	0.62	0.89	0.49	0.21	0.59	0.31	0.55	0.82	0.52	1.08	1.19	0.61	0.52	0.67	0.71	0.28	35.5	76.0	00.0	05.4	36.0
A. mabeei	33313	0.40	0.68	1.18	0.71	0.31	0.56	0.32	0.56	1.00	0.56	1.28	1.22	0.68	0.37	0.30	0.92	0.34	39.0	70.0	00.0	06.0	45.0
A. mabeei	33314	0.41	0.67	1.26	0.75	0.28	0.57	0.31	0.48	0.86	0.54	1.19	1.03	0.56	0.14	0.36	0.75	0.36	38.0	65.0	00.0	07.0	73.0
A. mabeei	33318	0.37	0.65	1.12	0.88	0.30	0.46	0.24	0.67	1.33	0.53	1.11	1.10	0.55	0.33	0.40	1.02	0.31	39.0	65.0	00.0	08.0	64.0
A. mabeei	33317	0.39	0.64	1.13	0.68	0.26	0.50	0.25	0.63	0.95	0.51	1.03	1.08	0.55	0.42	0.16	0.85	0.38	37.0	63.0	00.0	08.0	55.0
A. mabeei	33315	0.40	0.65	1.19	0.63	0.25	0.49	0.25	0.56	1.17	0.52	1.09	1.11	0.58	0.47	0.44	0.81	0.35	45.0	56.0	00.0	05.0	56.0
A. macrodactylum	13735	0.36	0.67	1.01	0.56	0.24	0.67	0.36	0.36	0.91	0.54	1.18	1.15	0.62	0.53	0.54	0.62	0.32	34.0	50.0	00.0	05.0	00.0
A. maculatum	23311	0.40	0.71	1.00	0.61	0.26	0.51	0.29	0.49	0.85	0.57	1.33	1.08	0.62	0.52	0.19	0.69	0.32	31.0	74.0	00.0	15.5	36.0
A. maculatum	32512	0.43	0.64	1.07	0.53	0.30	0.60	0.33	0.56	0.68	0.56	1.27	1.26	0.71	0.43	0.26	0.67	0.23	25.0	72.0	00.0	11.0	28.0
A. maculatum	32515	0.41	0.66	1.09	0.55	0.28	0.57	0.29	0.45	0.58	0.51	1.05	1.18	0.60	0.47	0.30	0.75	0.32	26.0	67.0	00.0	08.6	24.0
A. maculatum	32516	0.40	0.62	1.07	0.68	0.28	0.57	0.30	0.49	0.63	0.53	1.11	1.13	0.59	0.42	0.29	0.77	0.34	18.0	78.0	00.0	08.6	38.0
A. maculatum	32517	0.38	0.64	1.07	0.60	0.29	0.61	0.31	0.51	0.50	0.51	1.05	1.26	0.64	0.45	0.36	0.71	0.32	26.0	74.0	00.0	09.5	35.0
A. talpoideum	142135	0.46	0.61	0.92	0.58	0.28	0.57	0.30	0.52	0.85	0.52	1.09	1.14	0.59	0.56	0.25	0.70	0.36	36.5	80.0	00.0	11.0	00.0
A. talpoideum	142136	0.45	0.62	0.89	0.60	0.26	0.57	0.28	0.48	0.64	0.50	1.00	0.98	0.49	0.51	0.54	0.76	0.31	25.0	77.0	00.0	00.0	00.0
A. talpoideum	142137	0.42	0.65	0.78	0.73	0.38	0.71	0.34	0.44	0.78	0.48	0.93	1.18	0.57	0.39	0.58	1.00	0.37	36.5	72.0	00.0	00.0	00.0
A. opacum	23310	0.33	0.72	0.92	0.56	0.34	0.72	0.37	0.50	0.60	0.52	1.08	1.07	0.56	0.48	0.20	0.75	0.36	53.5	00.0	00.0	00.0	00.0
A. opacum	32511	0.38	0.62	1.10	0.69	0.11	0.88	0.43	0.51	0.68	0.18	0.93	1.24	0.60	0.39	0.27	0.88	0.28	37.0	00.0	00.0	05.8	00.0
A. opacum	32510	0.43	0.68	1.16	0.58	0.30	0.57	0.32	0.62	0.81	0.56	1.28	1.04	0.59	0.42	0.33	0.70	0.37	51.0	00.0	00.0	00.0	00.0
A. opacum	32313	0.48	0.67	0.96	0.66	0.31	0.59	0.34	0.54	0.73	0.57	1.33	1.18	0.68	0.46	0.31	0.86	0.28	65.0	00.0	00.0	05.3	45.0
A. texanum	13098	0.43	0.65	1.04	0.66	0.26	0.57	0.30	0.70	1.20	0.53	1.13	1.12	0.59	0.44	0.18	0.69	0.33	36.5	69.0	00.0	00.0	00.0
A. texanum	13099	0.39	0.63	0.99	0.74	0.31	0.68	0.36	0.43	1.05	0.53	1.15	1.26	0.67	0.41	0.32	0.69	0.51	35.0	59.0	00.0	00.0	00.0
A. texanum	13104	0.40	0.67	1.06	0.61	0.25	0.51	0.29	0.74	0.95	0.57	1.32	1.16	0.71	0.48	0.45	0.71	0.40	39.0	53.0	00.0	04.3	00.0
A. texanum	13101	0.39	0.67	0.98	0.76	0.29	0.62	0.35	0.78	1.00	0.57	1.32	1.24	0.71	0.40	0.40	0.85	0.38	36.0	79.0	00.0	07.0	00.0
A. texanum	13102	0.36	0.63	0.99	0.69	0.22	0.50	0.28	0.81	1.00	0.56	1.28	1.09	0.61	0.45	0.30	0.70	0.29	43.0	67.0	00.0	05.5	00.0
A. rosaceum	32507	0.45	0.65	1.11	0.49	0.25	0.59	0.32	0.42	1.13	0.54	1.17	1.17	0.63	0.67	0.44	0.63	0.27	32.0	61.0	00.0	08.5	64.0
A. rosaceum	32506	0.40	0.70	1.07	0.40	0.27	0.54	0.30	0.41	0.82	0.55	1.23	1.17	0.65	0.55	0.47	0.67	0.27	28.0	71.0	00.0	06.4	44.0
A. rosaceum	32505	0.46	0.69	0.97	0.51	0.26	0.61	0.31	0.46	0.92	0.52	1.07	1.18	0.61	0.55	0.39	0.73	0.24	24.0	74.0	00.0	00.0	00.0
A. t. tigrinum	31462	0.42	0.66	0.92	0.52	0.27	0.61	0.34	0.49	0.80	0.56	1.27	1.05	0.59	0.64	0.50	0.61	0.30	43.0	69.0	00.0	05.0	19.0
A. t. tigrinum	32513	0.44	0.68	0.97	0.49	0.28	0.61	0.32	0.16	0.74	0.53	1.11	1.01	0.53	0.53	0.31	0.65	0.36	39.0	73.0	00.0	06.6	20.0
A. t. tigrinum	32514	0.45	0.65	1.03	0.39	0.29	0.63	0.34	0.40	0.62	0.55	1.23	1.01	0.56	0.54	0.35	0.70	0.33	38.0	74.0	00.0	03.6	14.0
A. t. melanostictum	703	0.44	0.59	0.88	0.40	0.23	0.50	0.26	0.54	1.07	0.52	1.06	1.06	0.55	0.58	0.25	0.85	0.28	40.0	70.0	00.0	00.0	19.5
A. t. melanostictum	717	0.46	0.67	0.93	0.41	0.25	0.61	0.30	0.55	0.65	0.49	0.97	1.03	0.51	0.61	0.39	0.81	0.23	35.0	72.0	00.0	00.0	22.0
A. t. nebulosum	15106	0.39	0.49	0.94	0.47	0.27	0.62	0.34	0.52	0.70	0.53	1.11	1.07	0.56	0.58	0.46	0.79	0.33	63.0	70.5	00.0	08.0	55.0
A. t. nebulosum	32491	0.46	0.65	0.92	0.45	0.24	0.52	0.27	0.43	0.85	0.52	1.10	1.02	0.54	0.64	0.46	0.78	0.30	70.0	63.0	00.0	06.7	63.0
A. t. nebulosum	32493	0.40	0.59	0.87	0.47	0.32	0.61	0.32	0.39	0.72	0.52	1.09	1.00	0.52	0.53	0.32	0.83	0.32	53.0	59.0	00.0	10.5	56.0
A. t. nebulosum	15105	0.39	0.57	0.93	0.46	0.25	0.53	0.27	0.61	0.88	0.51	1.05	1.02	0.52	0.54	0.44	0.81	0.35	55.0	52.0	00.0	08.0	48.0
A. t. nebulosum	32520	0.45	0.62	0.94	0.44	0.23	0.56	0.27	0.52	0.96	0.49	0.94	1.09	0.53	0.63	0.38	0.72	0.35	57.0	52.0	00.0	06.7	69.0

[1]See text for explanation

Table 3. Binary Characters[1]

Species	Character Numbers																																								
	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63
Dicamptodon	0	0	1	0	0	1	1	1	0	1	1	1	1	0	1	0	0	1	1	0	0	0	1	0	0	0	0	0	1	1	0	0	1	0	0	0	1	0	0	1	0
Rhyacotriton	1	1	0	1	0	0	1	1	0	0	0	1	0	1	0	0	1	0	0	1	1	0	0	1	1	0	1	0	1	0	1	0	1	1	0	1	0	1	1	0	1
A. annulatum	1	0	0	0	1	0	0	1	0	0	0	1	0	0	0	0	1	0	0	0	1	0	0	1	1	2	0	1	0	1	0	1	1	0	0	1	0	0	0	0	1
A. cingulatum	0	0	0	0	1	0	0	1	0	0	0	1	0	0	1	0	0	0	0	1	0	1	1	0	1	0	1	0	1	0	1	0	1	1	0	0	0	0	0	0	1
A. gracile	1	1	1	0	0	0	1	1	0	0	0	1	0	1	0	0	0	0	0	0	1	0	1	0	1	0	1	0	1	0	1	1	1	0	1	0	0	0	0	1	
A. jeffersonianum	1	1	0	1	0	0	1	1	0	0	0	1	0	1	0	0	0	0	0	1	0	1	1	0	1	0	1	0	1	0	1	0	0	1	0	0	0	0	0	1	
A. mabeei	1	1	0	1	0	0	1	1	0	0	0	1	0	1	0	0	0	0	0	1	0	1	1	0	1	0	1	0	1	0	1	0	0	1	0	0	0	0	0	1	
A. macrodactylum	1	1	0	1	0	0	1	1	0	0	0	1	0	1	0	0	0	0	0	1	0	1	0	1	0	1	0	1	0	1	0	0	1	0	0	0	0	0	0	1	
A. maculatum	1	1	0	1	0	0	1	1	0	0	0	1	0	1	0	0	0	0	0	1	0	1	0	1	1	1	0	1	0	1	0	0	1	0	0	0	0	0	0	1	
A. talpoideum	1	1	0	1	0	0	0	1	0	0	0	1	0	1	0	0	0	0	0	1	0	0	1	0	1	1	0	1	0	1	0	1	0	0	0	1	0	0	0	0	1
A. opacum	1	1	0	0	0	1	0	0	0	0	0	1	0	0	0	0	1	0	0	0	1	0	1	1	0	1	1	0	0	1	1	0	1	0	0	0	0	0	0	1	
A. texanum	1	1	0	0	1	0	1	1	0	0	0	1	0	0	0	1	0	0	0	0	1	0	1	0	1	0	1	0	1	0	1	0	1	0	0	0	0	0	0	1	
A. rosaceum	1	1	0	0	1	0	1	1	0	0	0	1	0	1	0	0	0	0	1	0	1	0	1	1	0	1	1	0	1	0	1	0	1	0	1	1	0	0	0	0	1
A. tigrinum	1	1	0	0	1	0	1	1	0	0	0	1	0	1	0	0	0	0	0	0	1	0	1	0	1	0	1	0	0	0	0	0	1	0	0	0	0	0	0	1	
A. t. melanostictum	1	1	0	0	1	0	1	1	0	0	0	0	1	1	0	0	0	0	0	0	1	0	1	0	1	0	1	1	0	0	1	1	0	0	0	0	0	1	0	0	0	1
A. t. nebulosum	1	1	0	0	1	0	1	1	0	0	0	0	1	1	0	0	0	0	0	0	1	0	1	0	1	0	1	1	0	0	0	0	0	1	0	0	0	0	0	0	1

[1]See text for explanation

Depressor Mandibulae

The depressor mandibulae originates on the squamosal, the otic capsule, and the fascia cephalodorsalis and inserts on the posterior tip of the mandible. It is the major jaw-lowering muscle in salamanders.

Levator Mandibulae

This muscle consists of four portions, the levator mandibulae externus, the levator mandibulae posterior, and the levator mandibulae anterior, which is further divided into a superficial portion and a deep portion. The fibers intermingle considerably near the origins, and separation is rather difficult in some specimens.

The levator mandibulae externus lies lateral to the mandibular branch of the fifth cranial nerve and completely covers the deeper portion posteriorly. The fibers originate from the lateral margin of the squamosal and from the otic capsule, and they insert on the dentary and coronoid process of the prearticular. The levator mandibulae posterior is a short, triangular muscle which lies mesial and posterior to the mandibular nerve, originating on the squamosal, quadrate, and pterygoid and inserting on the articular and prearticular. Its distal fibers blend in with the tendon of the levator mandibulae anterior. The levator mandibulae anterior lies mesial to the mandibular branch of the fifth cranial nerve. The superficial portion, or temporalis, is a long, pinnate muscle arising by way of a tendon from the neural crest of the cervical vertebra and from fascia which is attached to the lateral margin of the parietal bone. The fibers extend in an anterior direction over the dorsal surface of the parietal and then turn sharply ventrad in front of the ear capsule to insert on the coronoid process of the prearticular. The deep portion of the levator mandibulae anterior originates on the lateral border of the frontal and parietal bones. The fibers of this deep portion blend in with those of the superficial portion, and together they insert on the dorsal margin of the prearticular. The fibers of this short, fan-shaped muscle extend in an almost vertical direction.

With respect to origins and insertions, the levator mandibulae is one of the most uniform muscles of those that are considered in this study. The size of this muscle varies considerably within the family as seen in *Dicamptodon* and *Rhyacotriton*, in which it is hypertrophied to the extent that part of it can be seen from a ventral view of the throat. Its action is to close the mouth by raising the mandible.

Interossaquadrata

According to Piatt (1940), this muscle, along with the subhyoideus, is derived from the interhyoideus. He further states that the subhyoideus and interossaquadrata are not found in the Ambystomidae; but, as mentioned in the introduction, we have found both muscles in each specimen dissected. The interossaquadrata is thick and narrow at its origin but spreads into a thin, fan-shaped muscle at its insertion. It originates on the ventral surface of the quadrate or on the hyoquadrate ligament which attaches the tip of the ceratohyal to the quadrate. The most posterior fibers may also attach on the tip of the mandible and lie ventral to the other fibers. These ventral fibers run caudo-mesiad, whereas the dorsal fibers extend anteriomesial. The fibers may meet at the midline in some specimens, or they may insert into the linea alba as the latter continues posteriorly from the intermandibularis posterior. The medial ends of the anterior fibers lie dorsal to the intermandibularis posterior.

Contraction of this muscle results in constriction of the hyobranchial skeleton and posterior mouth cavity.

Subhyoideus

The subhyoideus originates along the posterior tip of the ceratohyal. In *Rhyacotriton* this

line of origin extends a considerable distance anteriorly along the lateral margin of the ceratohyal. The insertion is also atypical in this species, being attached to the posterior edge of the mandible just lateral to the symphysis. In other ambystomids that are included in this study, the subhyoideus inserts along the dorsal surface of the linea alba and into fascia over the anterior end of the ceratohyal. The fibers fan out slightly so that the insertion is broader than the origin.

This muscle is apparently able to assist in bringing the hyobranchial apparatus forward in feeding.

Geniohyoideus

Originating on the posteroventral surface of the mandible just lateral to the symphysis, this muscle passes caudad as a rather narrow but stout band to insert onto the second basibranchial and onto the tendonous inscription that extends laterally from the base of the second basibranchial. The geniohyoideus can be seen in some specimens beneath the transparent linea alba. In many specimens, the anterior ends of these two muscles are separated, and the ventral portion of the genioglossus can be seen between them at the angle of the chin. The lateral edge of the genioglossus partially overlaps the origin of the geniohyoideus ventrally. In *Dicamptodon*, the two geniohyoideus muscles are not separated anteriorly.

This muscle acts to depress the lower jaw or the entire head. It also advances the second basibranchial cartilage.

Genioglossus

There are two parts to this muscle. The ventral portion fills the angle of the chin and originates on the posteroventral edge of the mandible, beginning at the symphysis and extending laterally for a millimeter or two. The fibers extend posteromesially to form a small triangle-shaped muscle at the point of the chin. These fibers insert into the aponeurosis lingualis which connects the root of the tongue with the first basibranchial cartilage. A few mesial fibers may also continue caudad for a short distance to attach to the anterodorsal edge of the first basibranchial and onto the otoglossal.

The dorsal portion of the genioglossus arises from the posterior edge of the mandible immediately dorsal to the origin of the ventral portion. The geniohyoideus must be removed in order to see the entire muscle since the latter overlaps the dorsal portion. If one were to proceed dorsad from the lateral edge of the ventral por-

tion of this muscle, he would encounter the ventral portion of the genioglossus, the geniohyoideus, and the dorsal portion of the genioglossus. The dorsal portion spreads out as a fan over the floor of the mouth. The medial fibers often pass posteriorly to insert onto the tip of the second radial, while the lateral fibers continue in a posterolateral direction to insert into the sides of the base of the tongue.

Contraction of this muscle helps to pull the tongue out of the mouth. It may also act to compress the glandular tissue of the tongue preparatory to opening the mouth and extending the tongue in feeding.

Subarcualis Rectus I

This muscle originates on the tip of the epibranchial, around which the fibers wrap, forming a muscular sheath. It then extends anteromedially, parallel with the ceratohyal to insert on the expanded anterior end of the latter and, therefore, loosely binds the epibranchial and the ceratohyal together. Along with the subhyoideus, this muscle acts to bring the hyobranchial apparatus forward in feeding.

Rectus Cervicis Superficialis

This muscle originates on the dorsal surface of the sternum and extends dorsal to the anterior end of the sternum, and to the coracoid cartilages. It continues forward as a thin, broad sheet ventral to the pericardium to attach to the second basibranchial and the tendonous inscription from which the geniohyoideus arises. It then continues forward as a thick, narrow band on either side of the midline to insert onto the posterior edge of the medial end of the ceratobranchial and onto the posterior end of the first basibranchial. The portion between the sternum and the second basibranchial has three transverse tendonous inscriptions in all of the specimens that are included in this paper, except for *Rhyacotriton* and *A. talpoideum*, in which there are only two. The omohyoideus is a muscle associated with the rectus cervicus superficialis. It arises from the ventral surface of the scapula and extends to the lateral edge of the rectus cervicis superficialis, attaching to the latter along the margin between the second basibranchial cartilage and the first or second tendonous inscription posterior to the second basibranchial. The deep fibers of the two rectus cervicis muscles intermingle considerably dorsal to the insertion of the omohyoideus. The omohyoideus is not included in the descriptions of each specimen. It is the only muscle of the throat region that links the hyobranchial

apparatus with the cartilages of the pectoral girdle. The omohyoideus serves to brace the rectus cervicis superficialis and to adduct the shoulder girdle (Tanner, 1952: 596).

The mesial fibers of the rectus cervicis superficialis contract to stabilize the second basibranchial, thereby providing a stable attachment for the insertion of the geniohyoideus. The lateral fibers assist the rectus cervicis profundus in retracting the tongue.

Rectus Cervicis Profundus

This muscle is actually a direct forward continuation of the rectus abdominus muscle which originates on the puboischium. The portion under consideration in this paper begins at the level of the sternum and continues forward in a position dorsolateral to the rectus cervicis superficialis. It lies alongside the pericardium and lateral to the second basibranchial. It then becomes thicker and narrower and passes through the space between the ceratobranchial cartilages. In all of the animals included in this paper, it proceeds forward to attach onto the posterior edge of the otoglossal cartilage. Since *Dicamptodon* does not have an annular otoglossal cartilage, this muscle is not attached in the same manner as in the other ambystomids. In this particular case, the forward portion of the rectus cervicis profundus attaches to the posterodorsal surface of the otoglossal plate, the latter forming a continuous structure with the second radial cartilages.

Myological studies of the Salamandridae (Francis, 1934; Özeti and Wake, 1969) indicate that the rectus cervicis profundus lies ventral to the hyoglossus muscle, but it is definitely dorsal to the hyoglossus in the Ambystomidae. In most specimens examined, the rectus cervicis muscle inserts on the otoglossal at a point that is anterior as well as dorsal to the hyoglossus.

When this muscle contracts, the entire hyobranchial apparatus is pulled posteriorly as in the retraction of the tongue. It may also function in flexion of the head.

Hebosteoypsiloideus

This muscle is a narrow band that takes its origin on the dorsal surface of one of the myosepta of the rectus cervicis profundus. From its origin, it proceeds anteriorly dorsal to the rectus muscles. It turns mediad at the level of the second basibranchial to insert on its dorsal surface. The function is to assist the rectus cervicis profundus in stabilizing and in retracting the second basibranchial.

Hyoglossus

This tiny muscle originates on the dorsal surface of the anterior end of the first basibranchial cartilage. There may be a few of the anteriormost fibers that also attach to the aponeurosis lingualis. The fibers are directed caudolaterally to insert on the lateral edge of the second radial cartilage. In some specimens there may be a few fibers which continue laterally for a short distance into the substance of the tongue.

These latter fibers may be homologous with the muscle referred to by Drüner (1901) as the basiradialis. In the ambystomids, however, we were unable to detect a separation along the course of the hyoglossus in any of the specimens observed.

As indicated above, this muscle lies ventral to the rectus cervicis profundus. This is in sharp contrast to the report by Francis (1934) for *Salamandra salamandra* in which he states that the rectus cervicis profundus lies ventral to the hyoglossus and that the former must be removed in order to expose the latter.

The contraction of the hyoglossus causes the second radial cartilage to swing in an anterodorsal direction, thereby elevating and protruding the pad of the tongue.

SPECIES DESCRIPTIONS

Pacific Giant Salamander

Dicamptodon ensatus (Eschscholtz)

Triton ensatus Eschscholtz, Zool. Atlas, Pt. 5, 1833, p. 6, pl. 22. *Dicamptodon*, Strauch, Mem. Acad. Sci. St. Petersb. Ser. 7, Vol. 16, 1870.

The range of this species is along the humid coastal regions of the Northwest. It extends from Santa Cruz County in California, north to the southern coastal region of British Columbia, and into northwestern Idaho and the Rocky Mountains of Montana. The ground color of the skin is brown, mottled or marbled with darker brown or black. This is the largest species of the Ambystomidae, transformed adults attaining occasionally a length of 300 mm. The body is stout, and the limbs are large and strong. The head is proportionately not as broad in this salamander as in many of the other ambystomids. There are 12 costal grooves, but they are poorly defined.

Vomerine teeth form a transverse series behind the internal nares and are interrupted by a narrow break at the midline where the series bends anteriorly. The teeth extend to the lateral margin of the internal nares.

HYOBRANCHIAL SKELETON (Fig. 1)

The first basibranchial is not separated from the radials by definite lines of articulation. It is truncate in shape and uniformly, though slightly, mineralized. In fact, the hyobranchium as a whole appears to be of a consistency intermediate between bone and cartilage. The first basibranchial is located in the center of the area circumscribed by the mandible.

This cartilage is shorter in relation to the total length of the hyobranchial skeleton than in any of the other ambystomids (Table 4). This is probably because the radials are especially long in this species. As seen in Table 5, the ratio of the first basibranchial length to first ceratobranchial length in *Dicamptodon* is the shortest of all the species being considered, with the exception of *A. annulatum*, *A. cingulatum*, and *Rhyacotriton*.

Table 4. Average ratios of length of first basibranchial to total length of hyobranchium.

Species	0	.1	.2	.3	.4	.5
Dicamptodon ensatus						
Rhyacotriton olympicus						
Ambystoma annulatum						
Ambystoma cingulatum						
Ambystoma gracile						
Ambystoma jeffersonianum						
Ambystoma mabeei						
Ambystoma macrodactylum						
Ambystoma maculatum						
Ambystoma talpoideum						
Ambystoma opacum						
Ambystoma texanum						
Ambystoma rosaceum						
Ambystoma tigrinum						
Ambystoma tigrinum melanostictum						
Ambystoma tigrinum nebulosum						

The first radial cartilages are long, curved, and jointed a little beyond their midpoint. Their distal ends articulate with the ceratohyals. They contain no distinct centers of ossification. The ratio of length of the first radial to the length of the first basibranchial is much greater in this species than in the other members of this family which we have studied (Table 6).

The second radials join the first basibranchial at their bases without a visible line of articulation, as mentioned above. These structures also unite with the otoglossal plate without any visible joint line. The otoglossal plate extends transversely between the two second radials and is tilted such that its anterior edge is more dorsal than its posterior edge. These structures appear to be composed of heavily calcified cartilage. In cutting into this tissue, one is impressed with the fact that it is denser than ordinary cartilage but less dense than bone.

The first ceratobranchial contains no distinct center of ossification and articulates, as in all of the species being studied in this paper, with the first basibranchial, the second ceratobranchial, and the epibranchial. As mentioned above, the first ceratobranchial is larger in relation to the first basibranchial than in all of the other species except *A. annulatum*, *A. cingulatum*, and *Rhyacotriton*.

No definite centers of ossification are found in the second ceratobranchials. The distal ends of these structures articulate with the first branchial arch at a point posterior to the articulation between the first ceratobranchial and the epibranchial. The ratio of the second ceratobranchial length to first ceratobranchial length is equal to that seen in *Rhyacotriton* and smaller than in the other ambystomids (Table 8).

A large center of ossification exists in the distal ends of the ceratohyals and is the largest percentage of ossification for this cartilage seen in the family (Table 1). The expanded anterior end is mostly cartilage, with a very slight amount of mineralization uniformly present throughout it.

The lateral arms of the second basibranchial are much larger than the anterior arm. No distinct center of ossification exists in this element.

The ratio of mandible length to width is greatest in this species (Table 9).

MUSCULATURE (Fig. 1)

Intermandibularis posterior originates along the dorsomedial edge of approximately the anterior three-quarters of the mandible. After ex-

tending in a transverse direction across the throat, the fibers insert into the linea alba. The posterior portion of this muscle overlaps the interossaquadrata ventrally. The ratio of the anteroposterior length of this muscle to the distance between the mental symphysis and the pectoralis muscle is greater in this species than in any of the others (Table 10).

Interhyoideus posterior originates on the ventrolateral surface of the quadrate, the lateral surface of the tip of the mandible, and the distal end of the squamosal. The fibers run transversely and slightly posteriorly to insert into the midventral line of fascia and into the skin and fascia of the gular fold. The anterior fibers form an almost indistinguishable margin with the posterior fibers of the interossaquadrata. The posterior edge of this muscle (the gular fold) is more posteriorly situated in this species than in other species (Table 11).

Depressor mandibulae originates in this species along the dorsal aspect of the squamosal and on the posteroventral surface of the otic capsule. It also attaches to the fascia cephalodorsalis. The fibers converge ventrally onto the posterior tip of the mandible.

Levator mandibulae is basically the same as that given above in the general statement of throat musculature of the Ambystomidae, except that the levator mandibulae posterior is not covered largely by the levator mandibulae externus. The majority of the latter muscle lies posterior to the levator mandibulae posterior. The tendon of insertion is tougher and larger than that seen in the other species. The overall size of the muscle, in fact, is hypertrophied as compared to other ambystomids, with perhaps the exception of *Rhyacotriton*, in which this particular muscle also appears to be enlarged.

Interossaquadrata originates on the medial aspect of the posterior tip of the mandible and the ventral surface of the quadrate immediately posterior to the mandibuloquadrate articulation. It inserts into the linea alba as the latter continues caudad from the intermandibularis posterior.

Subhyoideus originates on the posterior tip of the ceratohyal and wraps around the latter before proceeding forward parallel to the subarcualis rectus I. This is a thicker muscle than in the other species included in this investigation. It inserts into the dorsal fascia of the intermandibularis posterior. The interossaquadrata blends in with this muscle and overlaps it ventrally along the posterior one-third of its length.

Geniohyoideus takes its origin on the posterior edge of the mandible extending from the

Table 5. Average ratios of length of first basibranchial to length of first ceratobranchial.

Species	0	.1	.2	.3	.4	.5	.6	.7
Dicamptodon ensatus								
Rhyacotriton olympicus								
Ambystoma annulatum								
Ambystoma cingulatum								
Ambystoma gracile								
Ambystoma jeffersonianum								
Ambystoma mabeei								
Ambystoma macrodactylum								
Ambystoma maculatum								
Ambystoma talpoideum								
Ambystoma opacum								
Ambystoma texanum								
Ambystoma rosaceum								
Ambystoma tigrinum								
Ambystoma tigrinum melanostictum								
Ambystoma tigrinum nebulosum								

symphysis laterally for a distance of about 3 mm. The insertion is onto the anterior edge of the second basibranchial and laterally into the tendonous inscription that separates the geniohyoideus from the rectus cervicis superficialis.

Genioglossus is divided into ventromedial and dorsolateral portions as in the other species of this family. However, it appears to be a stouter muscle than in the others. It originates along the posterior edge of the mandible dorsal to the origin of the geniohyoideus. The medial fibers attach to the aponeurosis lingualis, and then proceed caudad to insert onto the anteroventral surface of the otoglossal plate. The lateral fibers overlap the tip of the second radial cartilage ventrally, and then insert into the adjacent fascia.

Subarcualis rectus I wraps around the posterior end of the epibranchial and forms a sheath which encloses the epibranchial. As the fibers pass forward, they follow the ceratohyal and spread out over the latter's expanded anterior end. The insertion is along the anterior edge of the ceratohyal.

Rectus cervicis superficialis originates on the

Table 6. Average ratios of length of first radial to length of first basibranchial.
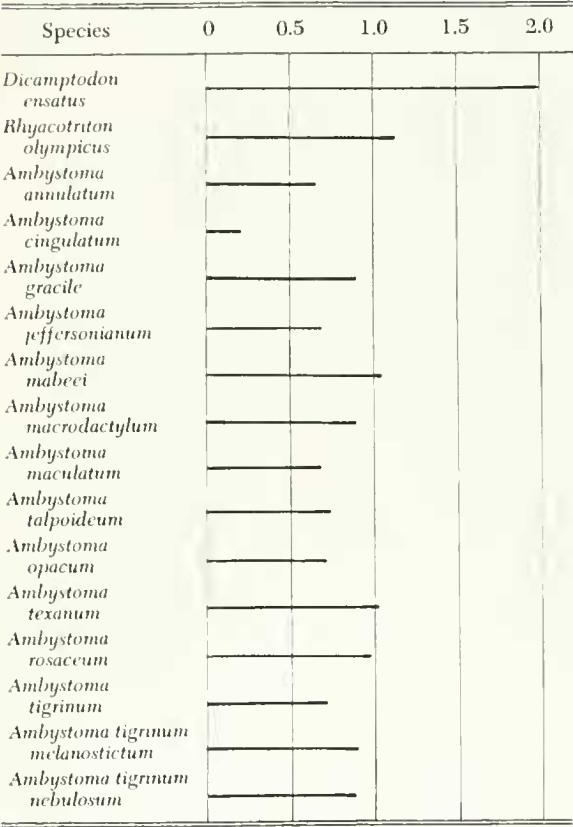
Species	0	0.5	1.0	1.5	2.0
Dicamptodon ensatus					
Rhyacotriton olympicus					
Ambystoma annulatum					
Ambystoma cingulatum					
Ambystoma gracile					
Ambystoma jeffersonianum					
Ambystoma mabeei					
Ambystoma macrodactylum					
Ambystoma maculatum					
Ambystoma talpoideum					
Ambystoma opacum					
Ambystoma texanum					
Ambystoma rosaceum					
Ambystoma tigrinum					
Ambystoma tigrinum melanostictum					
Ambystoma tigrinum nebulosum					

dorsal surface of the sternum and extends forward dorsal to the sternum, dorsal to the coracoid cartilages, and ventral to the pericardium. It attaches to the dorsal surface of the second basibranchial and laterally to the tendonous inscription from which the geniohyoideus arises. The superficial fibers of the portion which extends forward from this point insert into the posterior edge of the first ceratobranchial lateral to, but not inserting onto, the posterior tip of the first basibranchial. The deeper fibers continue forward to insert onto the posterior surface of the otoglossal plate ventral to the insertion of the rectus cervicis profundus.

Rectus cervicis profundus represents a direct anterior continuation of the rectus abdominus. From the level of the sternum, it passes forward along the dorsolateral edge of the rectus cervicis superficialis. It passes ventrally over the second ceratobranchial and dorsally over the first ceratobranchial. It inserts onto the posterodorsal surface of the otoglossal plate dorsal to the attachment of the rectus cervicis superficialis.

Hebosteoypsiloideus originates from the dorsal surface of the second myoseptum posterior to the second basibranchial. The fibers extend forward dorsal to the rectus cervicis profundus and then medially to insert onto the dorsal surface of the second basibranchial. The distal fibers in this species are strongly intermingled with those of the rectus cervicis profundus.

Hyoglossus. We have been unable to find a hyoglossus muscle in this species. The muscle which most nearly occupies the position of the hyoglossus is the posterior portion of the genioglossus, whose fibers extend in an anteroposterior direction for the most part. The lateral fibers of the genioglossus, however, do extend in a posterolateral direction as is seen in the hyoglossus of other salamanders.

Olympic Salamander.

Rhyacotriton olympicus (Gaige)

Ranodon olympicus Gaige, Occ. Papers Mus. Zool. Univ. Mich., No. 40, May 30, 1917, p. 2 pl. 1.
Rhyacotriton Dunn, Proc. N. Engl. Zool. Club, 7:56, 1920.

The Olympic Salamander is found in western Oregon and Washington. It has been collected in small springs and streams and among stones along the banks. This is a small ambystomid, occasionally attaining the size of 130 mm. It is characterized by its large, protuberant eyes, the horizontal diameter of which is equal to or greater than the length of the snout. The ground color is seal-brown with small white flecks distributed over the skin. The belly is yellow or orange in color. The tail is short and the gular fold is strongly developed. Costal grooves number 14 when the one in the axilla and the one in the groin are included. The vomerine teeth are formed into two strongly arched series that are separated at the midline. In the male, these series consist of fewer and larger teeth than in the female, and they extend in the male to a somewhat more lateral position in relation to the internal nares than in the female. The shape of the vent is different in the two sexes, the male being formed into squarish lobes which can readily be seen from either a dorsal or a ventral view, whereas in the female these lobes are considerably reduced in size.

Hyobranchial Skeleton (Fig. 2)

There is no ossification in the various components of the hyobranchium in this species (Table 1).

The first basibranchial is pear-shaped, but narrow. The width-to-length ratio is smaller, in

fact, than in any of the other ambystomids included in this study (Table 15). The distance posterior from the mental symphysis to the anterior edge of this structure in relation to the mandible length is exceeded only by *A. annulatum* (Table 12). The length of the first basibranchial is also small when compared to the total length of the first branchial arch (first ceratobranchial plus epibranchial) (Table 20).

The first radials attach to the anterior tips of the ceratohyals by a short ligament. These radials are delicate, cartilaginous rods projecting anterolaterad from the pointed anterior tip of the first basibranchial. The shortness of the first basibranchial is reflected in the high ratio of radial length to length of first basibranchial. This ratio is exceeded only by *Dicamptodon* (Table 6).

The second radials are approximately the same length as the first radials, but the former are curved dorsally to articulate with the otoglossal.

The first ceratobranchial is not uniformly wide along its length, being narrower at the anterior end and then becoming wider about midway along its length. It is flattened dorsoventrally.

The moderately long epibranchial forms a smooth continuation of the first ceratobranchial and is also flattened dorsoventrally. The second ceratobranchial is a narrow, smoothly curved rod of cartilage that forms a link between the posterior tip of the first basibranchial and the anterior end of the epibranchial. In relation to the first ceratobranchial, the second ceratobranchial is short when compared with the other species (Table 8).

The hyobranchial skeleton is shortened in an anteroposterior direction in this species. This is evident in the high ratio of ceratohyal length to total length of hyobranchium (Table 19).

The second basibranchial cartilage has a very small anterior projection. The ratio of anteroposterior length to side-to-side length of this element is smaller than in other species (Table 18).

MUSCULATURE (Fig. 2)

Intermandibularis posterior originates on the dorsomedial surface of the mandible. The fibers lie transversely for the most part, except for the posterior ones which are directed slightly caudad. The anterior portion appears almost as a separate muscle because it is a narrow band of continuous fibers extending across from one side to the other. Posterior to this band of muscle the linea alba, into which the remainder of

the fibers insert, is broad at first and then tapers to a point at the level of the posterior edge of this muscle. The geniohyoideus can be clearly seen through the broad portion of the linea alba.

Interhyoideus posterior is a thin ribbon-shaped muscle. The origin is broader than that seen in other species. The anterior fibers arise from the posterior tip of the mandible, while the remainder of the muscle originates from the fascia cephalodorsalis, which covers the lateral aspect of the depressor mandibulae, and from the lateral surface of the quadrate and the squamosal. It inserts into the gular fold and the midventral fascia. It appears to be a weaker muscle than the interhyoideus posterior of other species of the family. It especially appears small in contrast to the hypertrophied levator mandibulae of this species.

Depressor mandibulae originates from the fascia cephalodorsalis (posterior fibers), the upper posterolateral surface of the squamosal and from the posterolateral surface of the otic capsule. It inserts onto the posterior tip of the mandible.

Table 7. Average ratios of length of first ceratobranchial to total length of first branchial arch.

Species	0	.1	.2	.3	.4	.5	.6	.7	.8
Dicamptodon ensatus									
Rhyacotriton olympicus									
Ambystoma annulatum									
Ambystoma cingulatum									
Ambystoma gracile									
Ambystoma jeffersonianum									
Ambystoma mabeei									
Ambystoma macrodactylum									
Ambystoma maculatum									
Ambystoma talpoideum									
Ambystoma opacum									
Ambystoma texanum									
Ambystoma rosaceum									
Ambystoma tigrinum									
Ambystoma tigrinum melanostictum									
Ambystoma tigrinum nebulosum									

Levator mandibulae has its origin and insertions essentially the same as that given in the section on general musculature of the family. The size, however, is a departure from the condition seen in the other species. This muscle is hypertrophied as noted by the fact that it can be seen as a bulge behind the eye when viewed from the ventral surface. It can also be seen in *Dicamptodon* from a ventral view, but not to the same extent in the other species included in this study. The depressor mandibulae, which opens the mouth, is not enlarged in *Rhyacotriton* and perhaps closing the jaw with a powerful stroke is relatively more important in this species than opening the mouth, whereas this may not be the case in other species.

Interossaquadrata originates from the posterior surface of the quadrate, and ventral surface of the articulation between the ceratohyal and the quadrate. The middle fibers are attached, in addition, to the posterior tip of the mandible, and are hypertrophied to form a band of muscle extending directly mesiad. This muscle fans out over the venter of the throat and inserts into the fascia of the linea alba. The fibers from each side do not meet at the midline. It appears to be better developed and more easily separated from the subhyoideus than in other species of Ambystomidae.

Subhyoideus originates along the lateral margin of the ceratohyal beginning at a point about 1.0 mm from the posterior tip of this cartilage and extending forward about three-quarters of the distance to the anterior tip. It is a heavy muscle which is about as thick as the geniohyoideus, lying lateral and nearly parallel with the latter. The insertion is at a point on the posterior surface of the mandible immediately lateral to the origin of the geniohyoideus. This appears to be better developed than the subhyoideus in other species of the family.

Geniohyoideus is attached to the posterior surface of the mandible along a line which begins at the symphysis and extends laterally about 1.0 mm. The lateral fibers proceed directly caudad while the medial fibers are directed slightly mediad before turning in a caudal direction. This is a strong band of muscle, one on each side of the midline and overlapped ventrally by the intermandibularis posterior. It inserts onto the second basibranchial and in the tendonous inscription which separates this muscle from the rectus cervicis superficialis.

Genioglossus has two portions, a ventral part which is much the same as in other species, and a dorsal portion. Both of these appear to be slightly longer than in other species.

The ventral portion originates on the ventral and posterior surfaces of the mandible, beginning about 0.5 mm lateral to the symphysis and extending along this line of origin on the mandible for about 1.0 mm. The fibers converge to insert along the lateral edge of the ventral surface of the anterior end of the first basibranchial. It also sends a few fibers onto the otoglossal. This muscle is longer in this species than in others.

The dorsal portion originates from the same position as the ventral portion just described, except that it is immediately dorsal to the origin of the ventral portion. The lateral fibers pass caudad and slightly laterally to insert into the lateral part of the floor of the mouth dorsal to the subhyoideus belly. The medial fibers insert onto the ventral surface of the first basibranchial and the anterior edge of the first ceratobranchial. This muscle overlaps the radial cartilages ventrally.

Subarcualis rectus I attaches at its origin to the dorsal side of the posterior tip of the epibranchial, wraps around it, and encloses it in a sheath. The fibers continue obliquely in an anteromesial direction and fan out over the expanded anterior end of the ceratohyal. The insertion of these fibers is along the anterior margin of the ceratohyal. The overall position of this muscle appears to be more posterior than in the other species, the anterior tip not being very far anterior to the posterior tip of the mandible. In addition, these two muscles lie in a position in which the anterior ends tend to point strongly toward each other.

Rectus cervicis superficialis originates medially from the dorsal surface of the sternum and laterally along the tendonous inscription separating this muscle from the rectus abdominus. There are two transverse inscriptions along its length between the sternum and the second basibranchial. A small section of the pericardium is visible between these two muscles at the midline. The fibers that extend forward from the second basibranchial insert along the posterior edge of the medial end of the first ceratobranchial and onto the posterior tip of the first basibranchial. The sternum in this species is reduced to a small triangle with one angle facing anteriorly.

Rectus cervicis profundus originates technically on the puboischium. It is a broad sheet of muscle extending along the ventral body wall and continuing forward at the level of the sternum as a flat band of muscle that is overlapped partially on its medioventral surface by the rectus cervicis superficialis. It turns mediad and

passes through the arch formed by the two cera-
tobranchials, and then forward dorsal to the first
basibranchial to attach to the posterior edge of
the otoglossal.

Hebosteoypsiloideus originates from the dor-
sal surface of the rectus cervicis muscles at the
most anterior tendonous inscription of those in-
scriptions occurring between the sternum and
the second basibranchial. It is thin and narrow
and extends forward dorsal to the rectus cervi-
cis profundus for a short distance, where it turns
mediad across the rectus cervicis superficialis to-
ward the second basibranchial, upon whose dor-
sal surface it inserts.

Hyoglossus originates on the dorsal surface
of the anterior end of the first basibranchial and
along the lateral margin of the dorsal surface of
this cartilage. This small muscle is situated dor-
sal to the first basibranchial and ventral to the
insertion end of the rectus cervicis profundus.
The fibers extend laterally to insert onto the tip
of the second radial and into the fascia at the
sides of the base of the tongue.

RINGED SALAMANDER.

Ambystoma annulatum Cope

Amblystoma annulatum Cope, Proc. Amer.
Philos. Soc., Vol. 23, 1886, p. 525.

This is a strikingly marked salamander with
yellow spots and cross bars on a dark brown to
black ground color. The cross bars on the trunk
extend ventrad to the level of the legs, whereas
those on the tail reach the ventral edge. The
head is small and the tail long and slender. To-
tal length rarely exceeds 203 mm. There are 15
costal grooves, counting one each in the axilla
and groin. The vomerine teeth consist of two
short series that lie obliquely forward between
the internal nares to form an inverted V. Each
consists of three rows of 7 to 11 small, blunt
teeth. This species is abundant in parts of Ar-
kansas and Missouri and appears to be a bur-
rower, spending most of the year beneath the
surface of the ground..

HYOBRANCHIAL SKELETON (Fig. 3)

A definite center of ossification exists in the
first basibranchial. This center is located in an
anteromedial position, and constitutes a greater
percentage of the total volume of the first basi-
branchial than in any of the other species (Table
1). There are definite lines of articulation be-
tween this cartilage and the first radials. These
lines do not exist, however, between the first

Table 8. Average ratios of length of second cerato-
branchial to length of first ceratobranchial.

Species	0	0.2	0.4	0.6	0.8	1.0	1.2
Dicamptodon ensatus							
Rhyacotriton olympicus							
Ambystoma annulatum							
Ambystoma cingulatum							
Ambystoma gracile							
Ambystoma jeffersonianum							
Ambystoma mabeei							
Ambystoma macrodactylum							
Ambystoma maculatum							
Ambystoma talpoideum							
Ambystoma opacum							
Ambystoma texanum							
Ambystoma rosaceum							
Ambystoma tigrinum							
Ambystoma tigrinum melanostictum							
Ambystoma tigrinum nebulosum							

basibranchial and the second radials. The first
basibranchial is shaped like a slightly elongated
shield. This structure is situated in a more pos-
terior position in relation to the position of the
mandible than in other species (Table 12).

There is no ossification in the first radial car-
tilages. These structures are thin and taper to a
fine point. They do not attach to the anterior
end of the ceratohyal and they are not segment-
ed.

The second radials also are entirely carti-
laginous. They articulate with the otoglossal
cartilage at their distal tips. The otoglossal is a
thin bar of cartilage forming an arch which is
directed dorsally into the tongue.

The first ceratobranchial is devoid of bone.
In relation to the length of the first basibran-
chial, this structure is exceeded in length only
in *Rhyacotriton* and *A. cingulatum* (Table 5).

The epibranchial contains an ossified tip con-
stituting about 12 percent of its total volume
(Table 1), the remainder being cartilage. The
first ceratobranchial is long in relation to the
epibranchial, this ratio being exceeded only in
A. cingulatum (Table 13). The articulation be-

tween the epibranchial and the first cerato-branchial is almost indistinguishable.

The second ceratobranchial is longer in relation to the length of the first ceratobranchial in this species than in the others (Table 8) and contains no bone.

The ceratohyal shows no ossification. The width of this structure in relation to its length is exceeded only in *Dicamptodon* and *A. texanum* (Table 14).

The second basibranchial has a shape not seen in most other ambystomids. A small, posteriorly directed arm exists in addition to the other three, and the lateral arms are slightly expanded at their tips. More than half of the structure is cartilage, the lateral arms being almost entirely chondrified (Table 1).

The ratio of mandible length to width is exceeded only by *Dicamptodon* and *A. mabeei*, although it is equalled by *A. maculatum* and *A. cingulatum* (Table 9).

MUSCULATURE

Intermandibularis posterior originates along the dorsomedial surface of the mandible. The fi-

bers lie transversely and insert into the broad linea alba at the midline of the throat. The linea alba is wider than in the other species studied. The genioglossus is visible at the point of the chin, as in most other species.

Interhyoideus posterior originates from the fascia which is attached to the lateral edge of the posterior tip of the mandible, the quadrate, the squamosal, and the otic capsule. The posterior fibers arise in the fascia cephalodorsalis. The insertion is into the skin and fascia of the gular fold and into the linea alba at the midline. The anterior fibers blend in with the posterior fibers of the interossaquadrata.

Depressor mandibulae has its origin along the dorsal end of the squamosal, the ventral and posterior surfaces of the otic capsule, and the fascia cephalodorsalis. The fibers converge into a short, stout tendon which inserts onto the posterior tip of the mandible.

Levator mandibulae corresponds very closely to the description given in the section on general musculature.

Interossaquadrata originates from the ventral surface of the hyoquadrate ligament and from the quadrate bone immediately anterior to this ligament. The fibers fan out over the ventral surface of the throat, with the anterior fibers extending anteromedially over the ventral surface of the subarcualis rectus I, and the posterior fibers extending posteromedially to parallel the fibers of the interhyoideus posterior. The insertion is into the linea alba.

Subhyoideus originates on the ventrolateral margin of the posterior tip of the ceratohyal. It is thin and delicate, especially at its insertion. The posterior fibers are difficult to distinguish from those of the interossaquadrata. It lies over the ventral surface of the subarcualis rectus I and inserts into the dorsal surface of the fascia of the intermandibularis posterior.

Geniohyoideus originates along a line on the posterior edge of the mandible beginning at a point just lateral to the symphysis and extending laterally about 1.5 to 2.0 mm. This end is overlapped ventrally by the ventral portion of the genioglossus. The fibers extend directly caudad to insert on the second basibranchial cartilage.

Genioglossus originates along a line on the ventral surface of the mandible beginning at the symphysis and extending laterally over the ventral surface of the origin of the geniohyoideus. The fibers converge medially to form a strong band which contributes to the aponeurosis lingualis. Some of these fibers, in turn, continue distally to attach to the anterior end of the first basibranchial and to the otoglossal. Contraction

Table 9. Average ratios of mandible length to width.

Species	0	0.2	0.4	0.6	0.8	1.0	1.2
Dicamptodon ensatus							
Rhyacotriton olympicus							
Ambystoma annulatum							
Ambystoma cingulatum							
Ambystoma gracile							
Ambystoma jeffersonianum							
Ambystoma mabeei							
Ambystoma macrodactylum							
Ambystoma maculatum							
Ambystoma talpoideum							
Ambystoma opacum							
Ambystoma texanum							
Ambystoma rosaceum							
Ambystoma tigrinum							
Ambystoma tigrinum melanostictum							
Ambystoma tigrinum nebulosum							

Table 10. Average ratios of distance between mental symphysis and posterior edge of intermandibularis posterior to distance between mental symphysis and pectoralis.

Species	0	.1	.2	.3	.4	.5	.6
Dicamptodon ensatus							
Rhyacotriton olympicus							
Ambystoma annulatum							
Ambystoma cingulatum							
Ambystoma gracile							
Ambystoma jeffersonianum							
Ambystoma mabeei							
Ambystoma macrodactylum							
Ambystoma maculatum							
Ambystoma talpoideum							
Ambystoma opacum							
Ambystoma texanum							
Ambystoma rosaceum							
Ambystoma tigrinum							
Ambystoma tigrinum melanostictum							
Ambystoma tigrinum nebulosum							

terior end of the ceratohyal and insert along the latter's anterior edge.

Rectus cervicis superficialis originates from the dorsal surface of the sternum. The medial fibers attach to the second basibranchial and the lateral fibers form a thicker, narrower band which runs forward to insert along the posterior edge of the medial end of the first ceratobranchial. There are three transverse tendonous inscriptions in this muscle between the sternum and the second basibranchial.

Rectus cervicis profundus is actually an anterior continuation of the rectus abdominus. At the level of the sternum, this muscle extends anteriorly alongside of, and dorsal to, the rectus cervicis superficialis. Near its middle, the hebosteoypsiloideus can be seen along the border between the two rectus muscles. The rectus cervicis profundus becomes tendonous as it passes through the opening formed by the two ceratobranchials. This thin tendon then continues forward, dorsal to the first basibranchial, to attach to the medial section of the otoglossal. This tendon was seen only in this species and in *A. cingulatum*. The other species have fleshy insertions of this muscle on the otoglossal.

Hebosteoypsiloideus originates as a narrow band of muscle from the dorsal surface of the third inscription of the rectus cervicis profundus posterior to the second basibranchial. Its origin can be seen between the two rectus muscles. From here it extends forward dorsal to the medial edge of the rectus cervicis profundus and then turns medially to insert onto the dorsal surface of the central portion and anterior arm of the second basibranchial.

Hyoglossus originates on the dorsal surface of the anterior end of the first basibranchial and the adjacent fascia. Its fibers extend laterally and slightly posteriorly to attach along the posterior margin of the tip of the second radial. This is a small muscle.

of this muscle therefore serves to advance both of these cartilages. The ventral portion of the genioglossus is large in this species, as compared to the same muscle in most of the other species investigated.

The dorsal portion originates along the mandible just dorsal to the origin of the ventral portion. This muscle spreads out in a fan shape over the floor of the mouth. The medial fibers extend across the dorsal surface of the tips of the first radials and continue distally to insert along the posterolateral edge of the second radials. The lateral fibers insert into the fascia of the floor of the mouth.

Subarcualis rectus I originates along the dorsal edge of the tip of the epibranchial. The fibers radiate around this cartilage and enclose it in a sheath. They then continue forward in a medialanterior direction. When they reach the junction between the epibranchial and the second ceratobranchial, they lose their sheath shape and come to lie in a ventral position over the first ceratobranchial and the ceratohyal. Anteriorly, they spread out over the expanded an-

RETICULATED SALAMANDER.

Ambystoma cingulatum Cope

Amblystoma cingulatum Cope, Proc. Ac. Nat. Sci. Phil., 1867, p. 205.

This is a medium-sized species, less than 102 mm in total length. The ground color is black and has many small, gray spots which form a reticulated pattern on the dorsal surfaces of the head, trunk, and tail. Along the sides, these spots are concentrated into narrow vertical lines between the 13-14 costal grooves. Vomerine teeth are found in two short series, one on either side of the midline, and each contains about seven

teeth in two or three rows. This species is found from South Carolina to northern Florida and Alabama. Little is known about its habitat preference.

HYOBRANCHIAL SKELETON (Fig. 4)

The average ossification of the first basibranchial in the five specimens studied was 73 percent (Table 1). This ossification is centrally located, with a narrow margin of cartilage existing around the structure. No definite articulation lines were visible between the radials and the first basibranchial. This shield-shaped structure is located in a posterior position as compared to most of the other species. Only in *Rhyacotriton* and *A. annulatum* is the first basibranchial in a more posterior position (Table 12). It is shorter in relation to the total length of the hyobranchium than in all of the other species except in *Dicamptodon* and is wider in relation to its length than in other species (Tables 4 and 15).

The first radial cartilages are short, earlike projections without ossification. They are greatly reduced as compared to the other species (Table

6). They do not articulate with the anterior end of the ceratohyal.

The second radials are short and delicate and wholly cartilaginous. Their tips articulate with the otoglossal, the outline of which is pear-shaped rather than the usual annular shape.

In one of the five specimens which was dissected, the first ceratobranchial on each side contained a small ossification center on its medial end. The other four specimens were devoid of bone in this structure. In relation to the total length of the first branchial arch, the first ceratobranchial length is exceeded by no other species (Table 7); and, when compared to the length of the first basibranchial, it is only exceeded by *Rhyacotriton* (Table 5).

The joint between the first ceratobranchial and the epibranchial is difficult to locate, the two structures appearing to be well fused. Two of the five specimens contained no bone in the epibranchial, whereas the other three had an average of 15 percent ossification, the center of ossification in each case being located in the tip. The fraction of the total length of the first branchial arch that is contributed by the epibranchial is smaller than in other species (Table 16).

The second ceratobranchial contains no cartilage. When this structure (which is actually the second branchial arch) is compared in length to the first branchial arch (first ceratobranchial plus epibranchial), the ratio is found to be greater in this species than in others (Table 17).

The ceratohyal contains a long, narrow center of ossification running lengthwise at its posterior end. The bone in this structure amounts to an average of approximately 5 percent of the total volume. Two of the five specimens, however, had no ossification in the ceratohyal.

The second basibranchial has a small fourth arm projecting posteriorly. The cartilage portion of this structure is located on the lateral arms and is about 38 percent of the total volume. The anteroposterior length of the second basibranchial is almost half as long as the side-to-side length (Table 18).

The ratio of mandible length to mandible width is high for this species, being equalled by *A. maculatum* and *A. annulatum* and exceeded only by *Dicamptodon* and *A. mabeei* (Table 9).

MUSCULATURE (Fig. 4)

Intermandibularis posterior has the major portion originating along the dorsomedial surface of the mandible and inserting medially into the linea alba. The most anterior portion forms a stout band extending from the ventromedial surface of the mandible to the midline. The in-

Table 11. Average ratios of distance between mental symphysis and gular fold to distance between mental symphysis and pectoralis.

Species	0	.1	.2	.3	.4	.5	.6	.7	.8
Dicamptodon ensatus									
Rhyacotriton olympicus									
Ambystoma annulatum									
Ambystoma cingulatum									
Ambystoma gracile									
Ambystoma jeffersonianum									
Ambystoma mabeei									
Ambystoma macrodactylum									
Ambystoma maculatum									
Ambystoma talpoideum									
Ambystoma opacum									
Ambystoma texanum									
Ambystoma rosaceum									
Ambystoma tigrinum									
Ambystoma tigrinum melanostictum									
Ambystoma tigrinum nebulosum									

sertion of this anterior portion is more medial than the insertion of the remainder of the muscle. The genioglossus and the geniohyoideus can be seen passing dorsal to the forward edge of the anterior portion.

Interhyoideus posterior originates from a fascial sheet that is attached to the lateral aspect of the mandible tip, and from the quadrate, squamosal, and otic capsule. As in most of the other species, the posterior fibers attach to the fascia cephalodorsalis. The fibers extend postero-medially to form a prominent muscle whose insertion is along the skin of the gular fold and the midventral line of the throat. The anterior fibers blend in with those of the interossaquadrata.

Depressor mandibulae arises from the fascia cephalodorsalis, the dorsal and posterior surfaces of the squamosal, and from the ventral and posterior surfaces of the otic capsule. It inserts onto the posterior tip of the mandible.

Levator mandibulae is essentially the same as the description given earlier for the levator mandibulae in the general section on musculature.

Interossaquadrata originates on the lateral surface of the quadrate just anterior to the hyoquadrate ligament, from the lateral surface of the hyoquadrate ligament, and from the dorsal and lateral edges of the tip of the ceratohyal. The fibers wrap around the tip of the ceratohyal completely covering its lateral surface. They pass ventral to the subarcualis rectus I and fan out over the ventral surface of the throat. No noticeable boundary exists between the anterior fibers and those of the subhyoideus. The insertion is into the fascia along the midventral line of the throat and the dorsal surface of the fascia into which the intermandibularis posterior inserts.

Subhyoideus is a delicate muscle closely associated with the interossaquadrata. It originates along the lateral edge of the posterior end of the ceratohyal and extends anteromedially to insert into the dorsal surface of the fascia of the linea alba. The fibers at the origin lie dorsal to those of the interossaquadrata, but both muscles spread out over the throat; they form a broad fan-shaped structure, the anterior one-fifth of which is made up of fibers of the subhyoideus, whereas the remaining posterior portion is the interossaquadrata.

Geniohyoideus originates on the ventromedial surface of the mandible along a line beginning about 1.0 mm lateral to the symphysis and extending laterally about 1.5 mm. It is not over-lapped ventrally by the genioglossus but is crossed ventrally by the anterior band of the intermandibularis posterior. The medial fibers ex-

tend in a somewhat medial direction as they proceed caudad. The insertion is onto the second basibranchial cartilage and into the tendonous inscription which extends laterally from this cartilage.

Genioglossus is delicate when compared to the same structure in the other species investigated. It originates on the ventromedial surface of the mandible beginning at the symphysis and extending about 1.0 mm laterally. The fibers extend caudad to attach to the aponeurosis lingualis but continue on as a narrow band to insert onto the anterior edge of the first basibranchial and onto the otoglossal.

The dorsal portion originates along the mandible from a position immediately dorsal to the origin of the geniohyoideus. The fibers insert along the base of the anterior margin and the sides of the tongue. The medial fibers extend directly caudad to insert onto the second radial cartilage.

Subarcualis rectus I originates on the dorsal surface of the posterior tip of the epibranchial and then wraps around and encloses the epi-

Table 12. Average ratios of distance between mental symphysis and anterior edge of first basibranchial to mandible length.

Species	0	.1	.2	.3	.4	.5	.6	.7	.8	.9	1.0
Dicamptodon ensatus											
Rhyacotriton olympicus											
Ambystoma annulatum											
Ambystoma cingulatum											
Ambystoma gracile											
Ambystoma jeffersonianum											
Ambystoma mabeei											
Ambystoma macrodactylum											
Ambystoma maculatum											
Ambystoma talpoideum											
Ambystoma opacum											
Ambystoma texanum											
Ambystoma rosaceum											
Ambystoma tigrinum											
Ambystoma tigrinum melanostictum											
Ambystoma tigrinum nebulosum											

Table 13. Average ratios of length of first cerato-branchial to length of epibranchial.

Species	0	0.5	1.0	1.5
Dicamptodon ensatus				
Rhyacotriton olympicus				
Ambystoma annulatum				
Ambystoma cingulatum				
Ambystoma gracile				
Ambystoma jeffersonianum				
Ambystoma mabeei				
Ambystoma macrodactylum				
Ambystoma maculatum				
Ambystoma talpoideum				
Ambystoma opacum				
Ambystoma texanum				
Ambystoma rosaccum				
Ambystoma tigrinum				
Ambystoma tigrinum melanostictum				
Ambystoma tigrinum nebulosum				

branchial in a muscular sheath. This sheath continues anteromedially to the level of the cerato-hyal where it leaves the first ceratobranchial and spreads out over the ventral surface of the cera-tohyal. It inserts along the forward margin of the expanded anterior end of the ceratohyal.

Rectus cervicis superficialis originates on the dorsal surface of the sternum and extends forward ventral to the pericardium forming a thin, broad sheet. Between the sternum and the second basibranchial there are three transverse inscriptions. The portion which continues forward from the second basibranchial is narrower and thicker than the posterior portion. The anterior portion attaches to the anterior edge of the lateral tip of the second basibranchial and the adjacent tendonous inscription, and the fibers proceed anteromedially to insert along the posterior edge of the medial end of the first ceratobran-chial and along the lateral edge of the posterior tip of the first basibranchial.

Rectus cervicis profundus lies dorsolateral to the rectus cervicis superficialis, and its shape is essentially the same as the latter. It is actually a continuation of the rectus abdominus, and so the origin is, technically, the puboischium. The portion extending anteriorly from the second basibranchial is also narrower and thicker than the posterior portion. This anterior portion passes between the ceratobranchials and dorsal to the first basibranchial. At this point, the fibers converge into a thin, narrow tendon which inserts onto the medial section of the otoglossal. The tendon is 1.5 to 2.0 mm in length.

Hebosteoypsiloideus originates as a thin, narrow muscle from the dorsal surface of an incription on the rectus cervicis profundus. The particular inscription is the second one posterior to the second basibranchial. The fibers extend directly anterior at first, and then turn medially, dorsal to the rectus cervicis superficialis, and insert onto the dorsal surface of the second basi-branchial.

Hyoglossus is small, being slightly less than 1.0 mm in length. It originates from the dorsal surface of the anterior end of the first basibran-chial and extends laterally to insert on the tip of the second radial.

NORTHWESTERN SALAMANDER.

Ambystoma gracile (Baird)

Siredon gracilis Baird, Pacif. R. R. Rep., Vol. 10, Williamson's Route, Pt. 4, No. 4, 1859, p. 13, pl. 44, fig. 2.

The range of this species is from northern California to British Columbia. It is found in damp habitats and has been collected rather frequently under logs and bark, except during the breeding season, at which time it resorts to ponds and slow streams. It is less than 195 mm in total length. Probably the most distinguishing characteristic is the large, raised, kidney-shaped parotid glands behind the eyes. There is also a glandular region along the dorsal ridge of the tail. The color is dark brown; however, the head and tail may be slightly lighter. Some may be marked dorsally with yellow spots or flecks. There are 11 costal grooves, counting one each in the axilla and groin. The legs are large and strong. In contrast to most *Ambystoma* the ventral edge of the tail tends to be knifelike, while the dorsal edge is rounded. Vomerine teeth are in a transverse line which may be broken into three or four series.

HYOBRANCHIAL SKELETON (Fig. 5)

The first basibranchial is a rod-shaped structure lying in the center of the area outlined by the mandible. It contains no bone and has definite lines of articulation with the radials.

The first radials are moderately long and attached to the anterior edge of the ceratohyals by a ligament. They contain no bone.

The second radials are thin, cartilaginous rods that curve dorsally to attach to the annular-shaped otoglossal. Neither the second radial nor the otoglossal cartilages contains bone.

There is also a lack of bone in the first ceratobranchial, the second ceratobranchial, the epibranchial, and the ceratohyal. The only element which is ossified is the second basibranchial, which averages 78 percent bone for the two specimen studied (Table 1).

The ceratohyals are wide, being exceeded in a width-to-length ratio only by *Dicamptodon*, *A. annulatum*, *A. mabeei*, and *A. texanum* (Table 14).

The second basibranchial, as mentioned above, is the only ossified portion of the hyobranchium, the cartilage being located on the tips of the two lateral arms. This structure is strongly triradiate, the anterior arm being almost as long as the two lateral ones.

Only in three cases have we found a smaller ratio of mandible length to mandible width than in *A. gracile*. Those three are *A. talpoideum*, *A. t. nebulosum*, and *A. t. melanostictum*, the shortest being found in *A. talpoideum* (Table 9).

Masculature (Fig. 5)

Intermandibularis posterior has its origin along the dorsomedial surface of the rami of the mandible. The fibers extend transversely to insert into the fascia of the linea alba. A small area at the point of the chin is open so that the ventral portion of the genioglossus is visible. The posterior fibers overlap the anterior end of the interossaquadrata. The anterior fibers of this muscle are continuous across the midventral line. They constitute a band that is 2.0 mm wide at the midline.

Interhyoideus posterior originates in fascia that is attached to the posterior tip of the mandible, quadrate, squamosal, and the otic capsule. The posterior fibers arise from the fascia cephalodorsalis. The fibers spread out as they pass obliquely caudomedially to insert along the skin of the gular fold and the midventral line of fascia.

Depressor mandibulae takes its origin from the squamosal bone, attaching along its entire posterolateral surface except for the ventral 1-2 mm. It also arises from the lateral surface of the otic capsule and from the fascia cephalodorsalis. The fibers converge onto the posterior tip of the mandible.

Levator mandibulae corresponds to the description given earlier in the general section on musculature except that the fibers of the levator mandibulae externus and the levator mandibulae posterior intermingle considerably, making it difficult to separate these two portions.

Interossaquadrata originates from the ventral surface of the quadrate just anterior to the hyoquadrate ligament and from the ventral surface of the hyoquadrate ligament itself. A few fibers are also attached to the ventral aspect of the posterior tip of the ceratohyal. The anterior fibers extend anteromedially over the subarcualis rectus I, the medial fibers extend directly medially, and the posterior fibers extend caudomediad. These posterior fibers lie parallel with the anterior fibers of the interhyoideus posterior. It inserts into the median raphe of the throat.

Subhyoideus attaches along the ventrolateral margin of the posterior 2-3 mm of the ceratohyal. It becomes a thin muscle as it fans out over the anterior end of the subarcualis rectus I and is easily removed from the intermandibularis posterior as the deeper layers are exposed. It is readily distinguished from the interossaquadrata

Table 14.   Average width to length ratios of ceratohyal.

Species	0	.1	.2	.3	.4
Dicamptodon ensatus					
Rhyacotriton olympicus					
Ambystoma annulatum					
Ambystoma cingulatum					
Ambystoma gracile					
Ambystoma jeffersonianum					
Ambystoma mabeei					
Ambystoma macrodactylum					
Ambystoma maculatum					
Ambystoma talpoideum					
Ambystoma opacum					
Ambystoma texanum					
Ambystoma rosaceum					
Ambystoma tigrinum					
Ambystoma tigrinum melanostictum					
Ambystoma tigrinum nebulosum					

at its origin but blends in with the latter near the insertion. The insertion is by way of the dorsal surface of the fascia of the intermandibularis posterior.

Geniohyoideus originates from the posterior edge of the mandible along a line which begins about 1.5 mm lateral to the symphysis and extends laterally for approximately 1.0 mm. The anterior end of this muscle is overlapped along its medial edge by the ventral portion of the genioglossus. The lateral fibers extend directly caudad, whereas the medial fibers lie in a mediocaudal direction for a short distance before continuing directly caudad. Insertion is onto the second basibranchial cartilage, with the lateral fibers attaching into the tendonous inscription of the rectus cervicis superficialis.

Genioglossus originates in two parts, the ventral portion from the ventral and posterior surfaces of the mandible beginning at the symphysis and extending laterally about 2.5-3.0 mm. The fibers extend caudomedially for a short distance, overlapping the anteromedial end of the geniohyoideus as indicated above. Insertion is into the aponeurosis lingualis. A few fibers also continue on to the first basibranchial and the otoglossal. This latter portion is undivided.

The dorsal portion of the genioglossus originates along the posterior surface of the mandible from the symphysis to a point about 3-4 mm lateral from the symphysis. The lateral fibers proceed dorsal to the tip of the first radial and attach into the fascia that forms the floor of the mouth. The medial fibers insert onto the posterior edge of the lateral half of the second radial.

Subarcualis rectus I originates along the dorsal edge of the tip of the epibranchial. These fibers form a strong sheath around the epibranchial and then extend forward over the ventral surface of the ceratohyal. The insertion is along the anterior margin of the expanded end of the ceratohyal.

Rectus cervicis superficialis originates along the lateral edge of the dorsal surface of the sternum and from the tendonous inscription which separates this muscle from the rectus abdominus. It inserts onto the dorsal surface of the second basibranchial and then extends forward onto the posterior end of the first basibranchial and the posterior edge of the medial end of the first ceratobranchial.

Rectus cervicis profundus is actually a continuation of the rectus abdominus. It continues forward at the level of the sternum as a flat band and is situated dorsolaterally with respect to the rectus cervicis superficialis. The fibers turn slightly medially at the level of the second basi-

branchial and then pass through the opening between the ceratobranchials, where they extend dorsal to the first basibranchial and the hyoglossus and finally inserts along the posterior edge of the otoglossal.

Hebosteoypsiloideus consists of a narrow band of fibers arising from the dorsal surface of the second myoseptum of the rectus cervicis profundus posterior to the second basibranchial. It lies along the dorsomedial edge of the rectus cervicis profundus and extends forward and medially to insert along the lateral edge of the dorsal surface of the anterior arm of the second basibranchial cartilage. Like *A. talpoideum* it makes no insertion onto the lateral arms of the second basibranchial.

Hyoglossus originates from the dorsal surface of the anterior end of the first basibranchial and along the lateral edge of this cartilage to the base of the second radial. The anterior fibers extend laterally and posteriorly to insert onto the posterolateral edge of the second radial. The posterior fibers extend more directly lateral and insert into the fascia adjoining the second radial.

JEFFERSON'S SALAMANDER.

Ambystoma jeffersonianum (Green)

Salamandra jeffersoniana Green, Contr. Maclur. Lyc., Vol. 1, No. 1, Jan. 1827, p. 4, pl. 1, fig. 1.

This is a rather slender species which may attain a length of 185 mm. Adults have faint bluish markings on the sides. The ground color is dark brown. There are 12 costal grooves and a prominent gular fold. Toes are very long and slender. The vomerine teeth form a transverse line that is interrupted back of the internal nares and occasionally at the midline. The range extends from Hudson Bay south to Virginia. It is found westward to Wisconsin, Illinois, and Arkansas.

HYOBRANCHIAL SKELETON (Fig. 6)

The first basibranchial is shaped like an elongated pear when viewed from a ventrodorsal direction and is a flat oval when viewed in cross section. It contains a central mass of bone amounting to about 37 percent of the total volume (Table 1). Definite lines of articulation exist between this structure and the radials. There are only four other species in which the first basibranchial is more anteriorly located (Table 12).

The first radial cartilages contain no bone and are attached to the anterior tips of the ceratohyals by small ligaments. These radials are

short in relation to the length of the first basibranchial. This ratio is the same in *A. maculatum* and smaller only in *A. cingulatum* (Table 6).

The second radials are broad at their bases and taper quickly to fine tips which articulate with the tips of the otoglossal. The otoglossal is annular in shape, and neither the second radials nor the otoglossal contains bone. There are no centers of ossification located on the first ceratobranchials.

The epibranchials are long and contain bone only in their tips. It is because of their length that the length ratio of the first ceratobranchial to epibranchial is so small (Table 13). Only in *Dicamptodon*, *A. talpoideum*, *A. t. nebulosum*, and *A. t. melanostictum* is this ratio smaller. An average of more than one-third of the volume of the epibranchial is ossified (Table 1).

No bone is found in the second ceratobranchial. These cartilages are moderately long as indicated by the fact that the length ratio of the second ceratobranchial to the first ceratobranchial is greater only in four other species—*A. annulatum*, *A. maculatum*, *A. rosaceum*, and *A. texanum* (Table 8).

There is a center of ossification in the posterior tip of each ceratohyal. The average percent of ossification is 6.4 (Table 1). These cartilages are rather narrow when compared to the ceratohyal width-to-length ratios of the other species (Table 14).

Only the tips of the lateral arms of the second basibranchial are chondrified. The structure is distinctly triradiate in shape, and averages 80 percent bone.

Musculature (Fig. 6)

Intermandibularis posterior originates along the dorsomedial surface of the rami of the mandible. A small area at the point of the chin is open through which the genioglossus can be seen. The fibers extend medially to insert into the fascia of the linea alba. The posterior fibers also extend slightly caudad to overlap the anterior end of the interossaquadrata.

Interhyoideus posterior originates in fascia, which is attached to the posterior tip of the mandible, the quadrate, the squamosal, and the otic capsule. Posterior fibers also originate in the fascia cephalodorsalis. The fibers fan out over the throat to insert into the skin of the gular fold and the midventral fascia. The anterior fibers blend in with those of the interossaquadrata.

Depressor mandibulae originates along the posterolateral surface of the dorsal half of the

squamosal, the posterolateral surface of the otic capsule, and from the fascia cephalodorsalis. The insertion is onto the posterior tip of the mandible.

Levator mandibulae appears to have no significant differences between the configuration of this muscle and the description given in the section on general musculature.

Interossaquadrata originates along the posterior surface of the quadrate, and at this end of the muscle these fibers lie ventral to the origin of the subhyoideus. The insertion is into the fascia of the linea alba at the midventral line. The insertion end is very delicate and is easily pulled loose with the overlying intermandibularis posterior. As mentioned above, the posterior fibers blend in with those of the interhyoideus posterior so that a borderline between these muscles is located only by tracing the course of individual fibers back to their origin.

Subhyoideus originates along the ventrolateral margin of the posterior tip of the ceratohyal. This muscle passes forward and medially to blend in with the anterior edge of the interossaquadrata and inserts into the dorsal side of

Table 15. Average width to length ratio of first basibranchial.

Species	0	.1	.2	.3	.4	.5	.6	.7	.8
Dicamptodon ensatus									
Rhyacotriton olympicus									
Ambystoma annulatum									
Ambystoma cingulatum									
Ambystoma gracile									
Ambystoma jeffersonianum									
Ambystoma mabeei									
Ambystoma macrodactylum									
Ambystoma maculatum									
Ambystoma talpoideum									
Ambystoma opacum									
Ambystoma texanum									
Ambystoma rosaceum									
Ambystoma tigrinum									
Ambystoma tigrinum melanostictum									
Ambystoma tigrinum nebulosum									

the fascia of the intermandibularis posterior. This muscle is also very delicate and is easily removed inadvertently with the intermandibularis posterior.

Geniohyoideus takes its origin from a short line along the posterior surface of the mandible, the line beginning about 1.5 mm lateral to the symphysis and extending laterally for approximately 2.5 to 3.0 mm. The lateral fibers coming from this line extend directly caudad, whereas the medial fibers extend medially for a short distance and then proceed directly caudad. This muscle appears as a band proceeding between the chin and the second basibranchial into which it inserts. A few fibers also insert laterally into the tendonous inscription alongside of the second basibranchial.

Genioglossus originates in two parts, the ventral along a line on the posterior surface of the mandible. This line begins about 2.0 mm lateral to the symphysis and extends laterally along the mandible for about another 2.0 mm. This origin is immediately ventral to the medial half of the origin of the geniohyoidens. It inserts into the aponeurosis lingualis, with a few fibers continuing on to the first basibranchial and the otoglossal.

The origin of the dorsal portion of the genioglossus is along a line on the posterior surface of the mandible just dorsal to the origin of the geniohyoideus. The fibers extend laterally as well as caudally to insert into the floor of the mouth. The medial fibers extend caudally to the aponeurosis lingualis and then obliquely in a caudolateral direction to attach to the tip of the second radial.

Subarcualis rectus I originates on the posterior tip of the epibranchial and forms a sheath around the cartilage. It also extends out onto the ventral surface of the ceratohyal where it inserts along the anterior margin. The two ceratohyals almost touch each other at their anterior ends. They overlap the lateral edge of the anterior half of the first basibranchial, and these muscles, therefore, are also almost touching at that point.

Rectus cervicis superficialis originates on the posterior edge of the dorsal surface of the sternum and from the tendonous inscription which separates this muscle from the rectus abdominus. These fibers extend forward over the pericardium attaching to the second basibranchial and then continuing forward to insert onto the posterior tip of the first basibranchial and the posterior edge of the medial end of the first ceratobranchial cartilage.

Rectus cervicis profundus extends forward from the sternum as a stout band of muscle situated alongside of the rectus cervicis superficialis. It partially overlaps the latter dorsally as the two muscles move forward to the level of the second basibranchial. The archway between the two ceratobranchials serves as a passageway for this muscle as it continues forward to finally attach to the posterior edge of the otoglossal.

Hebosteoypsiloideus originates from one of the myosepta of the rectus cervicis profundus. The particular myoseptum is the second one posterior to the second basibranchial, from whose dorsal surface it arises as a narrow band and proceeds directly anteriorly. After a short distance, it turns medially to insert onto the dorsal surface of the second basibranchial.

Hyoglossus is a tiny muscle originating on the dorsal surface and lateral margin of the anterior end of the first basibranchial. It extends laterally to insert on the tip of the second radial cartilage and into the adjoining fascia.

MABEE'S SALAMANDER.
Ambystoma mabeei (Bishop)

Ambystoma mabeei Bishop, Journ. Elisha Mitchell Sci. Soc., Vol. 43, No. 3-4, 1928, p. 157.

This species inhabits rotted logs and bark in moist areas of the Carolinas and Georgia. The color above is deep brown, and the sides are covered with white or grayish flecks which become indistinct as they approach the dorsal surface, where they appear to be overlain with darker pigment. This salamander resembles *A. texanum* in size, color, and shape of the head. It reaches 102 mm in total length. The vomerine teeth form a transverse line that is broken back of the internal nares. There are 13 costal grooves, counting two that come together in the groin and one in the axilla.

HYOBRANCHIAL SKELETON (Fig. 7)

The first basibranchial cartilage in this species is pear-shaped when viewed from its ventral surface. It is a flat oval in cross section. The core is bony and is surrounded on all sides by a layer of cartilage. The average percent of ossification is 37. The first basibranchial is situated in a rather posterior position as compared to its position in other species, being exceeded in this respect only by *A. annulatum*, *A. cingulatum*, and *Rhyacotriton* (Table 12). The length of the first basibranchial as compared to the total length of the hyobranchium is greater in this species than in others except *A. Talpoideum*, *A. opacum*, and *Rhyacotriton* (Table 4).

The first radials are entirely cartilaginous and are relatively longer than in the other species ex-

Table 16. Average ratios of epibranchial length to length of first branchial arch.

Species	0	.1	.2	.3	.4	.5	.6
Dicamptodon ensatus							
Rhyacotriton olympicus							
Ambystoma annulatum							
Ambystoma cingulatum							
Ambystoma gracile							
Ambystoma jeffersonianum							
Ambystoma mabeei							
Ambystoma macrodactylum							
Ambystoma maculatum							
Ambystoma talpoideum							
Ambystoma opacum							
Ambystoma texanum							
Ambystoma rosaceum							
Ambystoma tigrinum							
Ambystoma tigrinum melanostictum							
Ambystoma tigrinum nebulosum							

cept *Dicamptodon* and *Rhyacotriton* (Table 6). Their tips are attached to the anterior tips of the ceratohyals by a short ligament, and a definite line exists at their base, indicating the point of articulation with the first basibranchial.

The second radials attach to the sides of the first basibranchial and then taper to a fine point in an anterodorsal direction. These distal tips articulate with the otoglossal, which is an annular-shaped rod of cartilage arched forward and dorsad into the tongue.

There is no bone in the first ceratobranchial. It is flattened dorsoventrally and forms a smooth arch which is continued distally by the epibranchial. The epibranchial averages 58 percent ossification, the bony portion constituting the distal end (Table 1).

The second ceratobranchial is entirely cartilage. Its distal end articulates with the medial side of the epibranchial at a point well posterior to the first ceratobranchial-epibranchial articulation.

The ceratohyal is longer in relation to the total length of the hyobranchium in this species than in other ambystomids, except for *Rhyacotriton* (Table 19). The average percent ossification for this structure is 6.8 (Table 1).

Only the extreme tips of the lateral arms of the second basibranchial are cartilage. The majority of the volume of this structure (63 percent) is bone. The anterior arm is much shorter than either of the lateral arms.

The ratio of the mandible length to mandible width is exceeded only by *Dicamptodon* (Table 9).

MUSCULATURE (Fig. 7)

Intermandibularis posterior originates on the dorsomedial surface of the mandible, and the fibers extend medially to the linea alba where they insert. The ventral portion of the genioglossus is visible at the point of the chin. The interossaquadrata and subhyoideus muscles are partly overlapped ventrally by this muscle. In contrast to most of the other species, the posterior fibers in this salamander exend almost directly transversely with only a slight deviation caudad.

Interhyoideus posterior is broad in this species, the anterior fibers extending directly mesially to the midline. The origin is by way of fascia which attaches to the posterior tip of the mandible, the squamosal, the quadrate, and the otic capsule and is also continuous with the fascia cephalodorsalis. The fibers pass over the mandible tip, cross the middle section of the subarcualis rectus I and insert into the skin and fascia of the gular fold and into the linea alba midventrally.

Depressor mandibulae fibers arise from the fascia cephalodorsalis, dorsal end of the squamosal and the posterior and ventral surfaces of the otic capsule. They converge to a short, tough tendon which inserts onto the posterior tip of the mandible.

Levator mandibulae consists of four portions as outlined in the general section on musculature.

Interossaquadrata originates on the posterior surface of the quadrate and the ventral surface of the ceratohyal-quadrate articulation. The fibers lie in an anteromedial direction. They insert into the fascia of the linea alba as it proceeds posteriorly from the intermandibularis posterior. This muscle is narrower in this species than in the others since there are no fibers extending in a posteromedial direction.

Subhyoideus originates from the ventral surface of the posterior tip of the ceratohyal. The fibers at the origin are dorsal to the interossaquadrata, but they proceed in a more anterior

direction than those of the interossaquadrata, resulting in a side-by-side location of their distal ends. From a point about midway along the length of these muscles, they appear as a single muscle since no definite line of separation is visible between them. The subhyoideus inserts into the dorsal surface of the fascia of the intermandibularis posterior.

Geniohyoideus originates from the posterior surface of the mandible along a line that begins at the symphysis and extends about 1.5 mm laterally. The medial fibers pass around the genioglossus at the point where the fibers of the latter converge and pass dorsad. From this point posteriorly, the fibers proceed directly caudad to insert onto the anteroventral surface of the second basibranchial and into the inscription that is continuous with the latter's lateral arm.

Genioglossus originates in two parts. The ventral portion arises along the ventral surface of the mandible, beginning at the symphysis and extending laterally about 1.5 mm. The origin is ventral to the origin of the geniohyoideus. The fibers converge toward the midline where they attach to the aponeurosis lingualis. From this point, they extend directly caudad and, together with the medial fibers of the dorsal genioglossus, form a broad sheet of muscle contributing substantially to the anterior half of the floor of the mouth. The insertion is onto the anterior edge of the first basibranchial and onto the otoglossal.

The origin of the dorsal genioglossus is immediately dorsal to the origin of the ventral portion. The fibers tend to fan out as they proceed caudad and in so doing form the broad sheet of muscle mentioned above. The medial fibers attach to the tip of the second radial. The lateral fibers insert into the fascia of the mouth floor at the base of the tongue.

Subarcualis rectus I originates from the dorsal edge of the epibranchial cartilage. The fibers form a sheath of muscle which completely encloses the epibranchial and then moves anteriorly parallel with the ceratohyal. At the level of the articulation between the epibranchial and the second ceratobranchial, the sheath opens up medially to permit the entrance of the second ceratobranchial into the sheath. From this point anteriorly, the muscle gradually loses its sheath-shape and comes to lie on the ventral surface of the ceratohyal. It inserts onto the anterior edge of this cartilage.

Rectus cervicis superficialis originates from the lateral half of the dorsal surface of the sternum and from the tendonous inscription that extends laterally from the sternum. There are three myosepta between the sternum and the second basibranchial. The omohyoideus arises along the lateral margin of this muscle between the first two of these myosepta. The rectus cervicis superficialis lies dorsal to the coracoids and ventral to the pericardium. A portion of the pericardium can be seen along the midventral line between these two muscles. The medial two-thirds of the fibers attach to the second basibranchial, but only the lateral half of these continues forward together with the remainder of the fibers to insert onto the posterior tip of the first basibranchial and the posterior edge of the medial end of the first ceratobranchial.

Rectus cervicis profundus is actually a forward continuation of the rectus abdominus and its origin is, therefore, from the puboischium of the pelvic girdle. There are three myosepta along the course of this muscle between the sternum and the insertion. It is situated in a position dorsal and lateral with respect to the rectus cervicis superficialis. The profundus is basically a thin, broad muscle, but the fibers become compacted into a thicker and narrower muscle belly at the level of the hyobranchium. The medial half of the opening between the ceratobranchials serves as a passageway through which the fibers pass. From this point, they proceed forward, dorsal to the first basibranchial and the second radial. They finally insert onto the otoglossal at a point well anterior to the first basibranchial.

Hebosteoypsiloideus is a narrow muscle which originates from the second tendonous inscription of the rectus cervicis profundus, posterior to the second basibranchial. It extends forward dorsal to the rectus cervicis profundus and then crosses over medially to insert onto the dorsal surface of the second basibranchial.

Hyoglossus is a small muscle seemingly hypertrophied in this species, as compared to the same muscle in other species. It originates on the dorsal surface of the anterior end of the first basibranchial and from the dorsal surface of the articulation between the first radial and the first basibranchial. The fibers converge slightly so that the insertion is narrower than the origin. They wrap around the ventral aspect of the tip of the second radial and insert along the latter's posterior edge.

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LONG-TOED SALAMANDER.

Ambystoma macrodactylum Baird

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Ambystoma macrodactyla Baird, Journ. Ac. Nat. Sci. Phila., Ser. 2, Vol. 1, 1849, p. 292.

This species has been found in breeding ponds, beneath rocks that are just above the waterline of these ponds, and beneath the loose bark of fallen trees. It is not unusual to find

them in the breeding ponds while these ponds are still icebound in the spring. The geographical range is along the Pacific Coast from California to British Columbia and Alberta, and then eastward into Idaho and Montana. It has also been reported in parts of Iowa. This is a slender animal whose total length may reach 128 mm. The chocolate brown to black ground color is topped by a median dorsal stripe that is dull tan to bright yellow in color. In some individuals, this stripe is greenish yellow. It may occur along the entire length of the animal's body, including head, trunk, and tail, or it may begin just behind the head. The usual number of costal grooves, including one each in the axilla and groin, is 12. The vomerine teeth form a broken line across the roof of the mouth. There are four sections to this line, the two middle ones being the longest, containing 9 to 10 teeth each, and lying wholly between the internal nares. The lateral sections contain 3 to 5 teeth each and are directed posterolaterally behind the inner nares.

HYOBRANCHIAL SKELETON (Fig. 8)

The first basibranchial cartilage is a pear-shaped structure with a central core of bone surrounded by a layer of cartilage. The bony portion constitutes 34 percent of the total volume (Table 1). There are definite lines of articulation with the radials. The first basibranchial is long when compared to the length of the first ceratobranchial. The ratio of lengths of first basibranchial to first ceratobranchial is exceeded only by A. opacum (Table 5). This structure is also rather narrow. The ratio of width to length is smaller only in Rhyacotriton (Table 15).

The first radials are long in relation to the first basibranchial length (Table 6). They are entirely cartilaginous and are connected to the ceratohyal tip by a short ligament.

The second radials are likewise entirely cartilaginous. They articulate with the tips of the otoglossal, the latter structure forming a cartilage ring which arches dorsad into the substance of the tongue.

The first ceratobranchial forms a smoothly arched bar of cartilage completely devoid of ossification. The epibranchial is also completely devoid of bone. It continues the smooth arch begun by the first ceratobranchial. The second ceratobranchial, like the first branchial arch, contains no bone.

A small tip of bone exists in the posterior end of the ceratohyal in this species and constitutes 5 percent of the total volume of this element (Table 1).

The triradiate second basibranchial was found to be 50 percent cartilage and was shorter from side-to-side in comparison to its anteroposterior length than the same structure in other ambystomids (Table 18).

Although the mandible length appears quite short, the ratio of length to width is actually smaller in several other species (Table 9).

MUSCULATURE (Fig. 8)

Intermandibularis posterior originates along the dorsomedial edge of the mandible. There are fibers lacking at the point of the chin, and consequently the genioglossus is visible there. The fibers lie mostly in a medial direction where they attach into the linea alba of the throat. The fibers from each side do not quite meet at the midline. The ratio of distance between the mental symphysis and the posterior edge of this muscle to the distance between the mental symphysis and the pectoralis muscle is smaller in this species than in any of the others (Table 10).

Interhyoideus posterior has a complex origin with the lateral fibers arising from the fascia cephalodorsalis, and the middle fibers attaching

Table 17. Average ratios of length of second ceratobranchial to total length of first branchial arch.

Species	0	.1	.2	.3	.4	.5	.6	.7	.8
Dicamptodon ensatus									
Rhyacotriton olympicus									
Ambystoma annulatum									
Ambystoma cingulatum									
Ambystoma gracile									
Ambystoma jeffersonianum									
Ambystoma mabeei									
Ambystoma macrodactylum									
Ambystoma maculatum									
Ambystoma talpoideum									
Ambystoma opacum									
Ambystoma texanum									
Ambystoma rosaceum									
Ambystoma tigrinum									
Ambystoma tigrinum melanostictum									
Ambystoma tigrinum nebulosum									

to the posterior tip of the mandible just anterior to the insertion of the depressor mandibulae. By way of fascia, this muscle also attaches to the lateral surface of the mandible tip, the lateral surface of the mandibulo-quadrate articulation, and the lateral surface of the ventral end of the squamosal. The fibers fan out over the posterior throat region to insert along the skin of the gular fold and into the midventral line of fascia, the linea alba.

Depressor mandibulae originates from the posterolateral edge of the squamosal except for the ventral 1-2 mm, which attaches to the fascia cephalodorsalis and the lateral surface of the otic capsule. It inserts onto the posterior tip of the mandible.

Levator mandibulae is essentially the same as that description given in the general musculature section of this paper.

Interossaquadrata originates on the posterior surface of the quadrate, the ventral surface of the articulation of the ceratohyal and the quadrate, and from the posterior tip of the mandible. The fibers spread out over the throat with the anterior fibers directed anteromedially and the posterior fibers in a posteromedial direction. The insertion is into the fascia of the linea alba.

Subhyoideus originates along the anteroventral edge of the posterior tip of the ceratohyal. It fans out as it proceeds forward over the throat and inserts into the dorsal fascia of the intermandibularis posterior. The posterior fibers blend in with those of the interossaquadrata so that no border is distinguishable between these two muscles.

Geniohyoideus originates along a line on the posterior surface of the mandible which begins about 1.0 mm lateral to the symphysis and extends laterally about 1.0 additional mm. The fibers pass caudad and mediad, and then directly caudad to form a stout band on either side of the midline. It inserts onto the second basibranchial and in the tendonous inscription that extends laterally from the arms of the second basibranchial.

Genioglossus has a ventral portion which originates on the ventral and posterior surfaces of the mandible, beginning at the symphysis and extending laterally approximately 1.0 mm. The fibers overlap the anterior end of the geniohyoideus and converge medially to attach themselves into the aponeurosis lingualis before continuing to attach to the anterior tip of the first basibranchial and the otoglossal.

The lateral fibers are directed laterally as well as caudad and form a thin sheet of muscle which inserts into the fascia forming the floor of the mouth. These fibers lie in a dorsolateral position with respect to the anterior end of the ceratohyal. The medial fibers proceed directly caudad into the aponeurosis lingualis and then to the tip of the second radial.

Subarcualis rectus I originates on the tip of the epibranchial cartilage, from which its fibers wrap around and enclose the latter in a muscular sheath and then continue forward over the ventral surface of the ceratohyal. The insertion is along the ventral surface of the anterior margin of the ceratohyal.

Rectus cervicis superficialis originates along the dorsal surface of the posterior end of the sternum and the tendonous inscription which separates this muscle from the rectus abdominus. The fibers extend forward ventral to the pericardium. In this species there is a large section of the pericardium which is exposed at the midline between the two rectus cervicis superficialis muscles. The second basibranchial is attached to this muscle and serves as a landmark between the thin, broad portion of the muscle and the anterior portion which becomes thick and nar-

Table 18. Average ratios of anterior to posterior length to second basibranchial to width of second basibranchial.

Species	0	.1	.2	.3	.4	.5	.6
Dicamptodon ensatus							
Rhyacotriton olympicus							
Ambystoma annulatum							
Ambystoma cingulatum							
Ambystoma gracile							
Ambystoma jeffersonianum							
Ambystoma mabeei							
Ambystoma macrodactylum							
Ambystoma maculatum							
Ambystoma talpoideum							
Ambystoma opacum							
Ambystoma texanum							
Ambystoma rosaceum							
Ambystoma tigrinum							
Ambystoma tigrinum melanostictum							
Ambystoma tigrinum nebulosum							

row. This anterior portion inserts onto the posterior tip of the first basibranchial and the posterior edge of the medial end of the ceratobranchial.

Rectus cervicis profundus at the level of the sternum extends forward alongside of and deep to the rectus cervicis superficialis. After passing dorsal to the omohyoideus, it turns slightly mediad and proceeds through the opening between the ceratobranchials to insert onto the posterior edge of the otoglossal.

Hebosteoypsiloideus originates as a narrow muscle on the dorsal surface of the rectus cervicis profundus. It is separated from the latter only by careful dissection since the fibers of these two muscles lie parallel with each other. It is from the second myoseptum posterior to the second basibranchial that this muscle arises. It crosses the rectus cervicis superficialis and then inserts onto the dorsal surface of the second basibranchial.

Hyoglossus is a small muscle situated between the dorsal surface of the first basibranchial and the ventral surface of the rectus cervicis profundus. It originates along the dorsolateral

edge of the first basibranchial between the anterior tip and the base of the second radial. The anterior fibers extend obliquely in a posterolateral direction whereas the posterior fibers extend directly laterad and converge with the former to insert onto the posterolateral edge of the second radial as it curves dorsad into the tongue.

Spotted Salamander.

Ambystoma maculatum (Shaw)

Lacerta maculata Shaw, Gen. Zool., Vol. 3, Pt. 1, 1802, p. 304.

The spotted salamander is distinguished by a row of large, round, yellow or orange spots occurring on either side of the middorsal line. The ground color is a deep bluish black. Males are usually more slender than females, and the former are readily recognized in the breeding season by the swollen vent. Total length reaches 206 mm. There are usually 12 costal grooves, a prominent gular fold, and, in this species, larger legs. The vomerine teeth extend across the roof of the mouth in a smoothly curved line immediately behind the internal nares. This line is sometimes interrupted at the midline and in back of the internal nares. The geographical range is from Nova Scotia to Wisconsin and southward to Florida, Louisiana, and Texas. They are found in ponds, slow moving streams, or temporary pools which offer spring breeding sites.

Hyobranchial Skeleton (Fig. 9)

The first basibranchial is a pear-shaped structure when viewed ventrally and has a central core of bone. In cross section it is flat oval in shape. The bone constitutes an average of about 25 percent of its volume (Table 1). There are lines of articulation visible between the first basibranchial and the radials.

The first radials are short in relation to the length of the first basibranchial. The only other species with a smaller ratio of length of first radial to length of first basibranchial is A. *cingulatum* (Table 6). No bone is found in these structures.

The second radials articulate with the otoglossal at their distal tips. The otoglossal forms a thin arch of cartilage extending dorsad into the tongue.

The first ceratobranchials are nearly straight, the only prominent curve in the first branchial arch occurring in the anterior half of the epibranchial. There is no ossification in either ceratobranchial.

Table 19. Average ratios of length of ceratohyal to total length of hyobranchium.

Species	0	0.1	0.2	0.3	0.4	0.5	0.6	0.7	0.8	0.9	1.0
Dicamptodon ensatus											
Rhyacotriton olympicus											
Ambystoma annulatum											
Ambystoma cingulatum											
Ambystoma gracile											
Ambystoma jeffersonianum											
Ambystoma mabeei											
Ambystoma macrodactylum											
Ambystoma maculatum											
Ambystoma talpoideum											
Ambystoma opacum											
Ambystoma texanum											
Ambystoma rosaceum											
Ambystoma tigrinum											
Ambystoma tigrinum melanostictum											
Ambystoma tigrinum nebulosum											

The epibranchial is ossified at its tip, the ossification making up an average of 32 percent of the total volume (Table 1). The width of this element is uniform along most of its length except near the tip where it tapers abruptly to a point.

The ratio of the lengths of the second ceratobranchial to the first ceratobranchial is high in this species, being exceeded only by *A. annulatum* (Table 8). This element is unossified.

The posterior tip of the ceratohyal is ossified and constitutes an average of 10.6 percent of the total volume (Table 1). The anterior tips overlap slightly at the midline.

The lateral arms of the second basibranchial are much longer than the anterior arm, and it is on these lateral tips that the cartilage is found. This cartilage constitutes 27 percent of the total (Table 1).

The mandible is longer than it is wide, the ratio of length to width averaging 1.06 for the five specimens of *A. maculatum* used in this study (Table 9).

MUSCULATURE (Fig. 9)

Intermandibularis posterior originates along the dorsomedial surfaces of the rami of the mandible. There is a small opening at the angle of the chin through which the genioglossus can be seen. This muscle overlaps the anterior end of the interossaquadrata and the anterior portion of the subhyoideus. The fibers pass, basically, in a transverse direction to the midventral line where they insert. There is no broad fascial sheet in this species occupying the midventral line as is seen in most other species.

In one of five specimens the anterior fibers of the intermandibularis posterior were continuous across the midline. This band was 0.7 mm wide at the midventral line.

Interhyoideus posterior originates on the fascia cephalodorsalis and on the posterior tip of the mandible immediately medial and anterior to the insertion of the depressor mandibulae. The majority of this muscle attaches by way of a fascial sheet to the lateral surface of the tip of the mandible, the lateral surface of the articulation between the mandible and the quadrate, and the lateral surface of the ventral end of the squamosal. This muscle inserts into the gular fold and midventral fascia of the throat.

Depressor mandibulae originates from the fascia cephalodorsalis, the lateral surface of the otic capsule, and the dorsal half of the lateral surface of the squamosa. The fibers converge to insert onto the posterior tip of the mandible.

Levator mandibulae has its origin and insertion essentially as in the description given in the section on general musculature.

Interossaquadrata originates from the posterior surface of the quadrate and the ventral surface of the articulation between the quadrate and the ceratohyal. The most posterior fibers also attach to the posterior tip of the mandible and lie ventral to the other fibers of this muscle. These ventral fibers extend caudomesially whereas the dorsal fibers extend anteromesially. The insertion is into the linea alba as it continues caudad from the intermandibularis posterior.

Subhyoideus originates from the dorsum of the posterior or distal tip of the ceratohyal and inserts into the dorsal fascia of the intermandibularis posterior.

Geniohyoideus originates along the posterior surface of the mandible along a line beginning just lateral to the symphysis and extends laterally approximately 3.0 mm, deep to the ventral portion of the genioglossus. This muscle is narrower anteriorly than posteriorly, and consequently the genioglossus is exposed along the midline in this species. There are some deep fibers which attach to the aponeurosis lingualis and extend posteriorly with the remainder of the muscle. The muscle inserts onto the second basibranchial and into the tendonous inscription which separates this muscle from the rectus cervicis superficialis.

Genioglossus has a ventral portion which originates on the ventral and posterior surfaces of the mandible beginning at the symphysis and extending laterally for about 3.0 mm. The fibers extend in a caudomedial direction to form a small triangular-shaped muscle. This portion of the genioglossus overlaps the anterior end of the geniohyoideus. The insertion is into the aponeurosis lingualis which continues caudad to attach to the anterior end of the first basibranchial cartilage. A few fibers continue along in association with the aponeurosis lingualis and insert onto the otoglossal.

The dorsal portion of this muscle attaches along the posterior edge of the mandible beginning at a point on the mandibular symphysis and extending laterally for about 2.0 mm. The fibers fan out as a thin sheet which contributes to the anterior floor of the mouth. The medial fibers extend caudad to insert onto the posterior edge of the second radial tip, while the lateral fibers continue caudad and laterally to attach into the fascia lateral to the base of the tongue. The aponeurosis lingualis, in this as well as most other species of this family, sends a slip onto the

Table 20.   Average ratios of length of first basibranchial to total length of first branchial arch.

Species	0	.1	.2	.3	.4
Dicamptodon ensatus					
Rhyacotriton olympicus					
Ambystoma annulatum					
Ambystoma cingulatum					
Ambystoma gracile					
Ambystoma jeffersonianum					
Ambystoma maheei					
Ambystoma macrodactylum					
Ambystoma maculatum					
Ambystoma talpoideum					
Ambystoma opacum					
Ambystoma texanum					
Ambystoma rosaceum					
Ambystoma tigrinum					
Ambystoma tigrinum melanostictum					
Ambystoma tigrinum nebulosum					

tip of the first radial cartilage and continues on to attach the first radial to the anterior tip of the ceratohyal.

Subarcualis rectus I originates on the tip of the epibranchial cartilage. It wraps around this tip and proceeds forward, medial to the angle of the jaw where it then begins to fan out into a thin sheet over the ventral surface of the ceratohyal. It inserts along the anterior margin of the ceratohyal.

Rectus cervicis superficialis originates from the dorsal surface of the sternum and the tendonous inscription which separates this muscle from the abdominal muscles posteriorly. It passes forward ventral to the pericardium. The medial fibers attach to the second basibranchial, which is actually partly imbedded in this muscle. The lateral fibers end on the tendonous inscription which extends outward from the lateral arms of the second basibranchial. At this point, the muscle continues forward again to become a thick band which inserts onto the hyobranchial skeleton. It inserts onto the posterior tip of the first basibranchial and the posterior edge of the first ceratobranchial where the latter articulates with the first basibranchial. It also sends fibers onto the dorsal surface of the base of the first ceratobranchial and the lateral portion of the dorsal surface of the posterior end of the first basibranchial.

Rectus cervicis profundus is extended forward alongside and dorsal to the rectus cervicis superficialis. At the level of the second basibranchial, it begins to turn medially and become thicker and narrower. It passes through the archway formed by the two ceratobranchials and continues forward dorsal to the first basibranchial to its insertion on the posterior edge of the otoglossal cartilage.

Hebosteoypsiloideus originates from the dorsal surface of the most posterior inscription on the rectus cervicis profundus. It extends forward dorsal to the latter until, at the level of the omohyoideus, it turns medially to cross the rectus cervicis superficialis dorsally and insert onto the dorsal surface of the second basibranchial.

Hyoglossus is a small triangular-shaped muscle which originates on the dorsal surface of the anterior end of the first basibranchial and along the lateral edge of the dorsal surface of this cartilage to the base of the second radial. The fibers converge to insert on the tip of the second radial where the latter turns dorsad to join the otoglossal. A few fibers, in addition, continue laterally to attach to the fascia of the floor of the mouth.

MOLE SALAMANDER.

Ambystoma talpoideum (Holbrook)

Salamandra talpoidea Holbrook, N. Amer. Herp., Ed. 1, Vol. 3, 1838, p. 117, pl. 29.

This is a small species with a broad, depressed head, a rounded body, and a short tail. Total length ranges up to 97 mm. It has 10 costal grooves, counting one each in the axilla and groin. Vomerine teeth form three distinct series, the middle one being situated some distance posterior to the internal nares. The lateral series begin a short distance behind the internal nares and extend a short distance laterally. The ground color is dark brown dorsally, becoming bluish gray along the lower sides. Small bluish white flecks are scattered over the surface of the skin, becoming numerous enough on the lower sides to form large patches. The range of this species is along the Southeast and Gulf Coasts of the United States from North Carolina to Louisiana and northward to Illinois. It has also been found in Oklahoma, Arkansas, and Texas.

HYOBRANCHIAL SKELETON (Fig. 10)

The ossification center which makes up the core of the first basibranchial amounts to an average of 32.6 percent of the total volume. This structure is pear-shaped when viewed from the ventral surface, and the cross sectional area is a flat oval. The lines of articulation with the radials are distinct. The first basibranchial is long compared to the total length of the entire hyobranchium and as compared to the length of the first ceratobranchial (Tables 4 and 5).

There is no bone in the radials. The first pair is free from the ceratohyals and unjointed. The second pair attaches to the tips of the otoglossal. The otoglossal cartilage is a smoothly curved rod of cartilage which arches into the tongue from below.

The first ceratobranchial is a slightly curved, unossified, rod of cartilage. It is flattened dorsoventrally. The major bend in the first branchial arch occurs in the anterior half of the epibranchial. The latter is also unossified. The epibranchial length in relation to the length of the entire first branchial arch and in relation to the length of the first ceratobranchial is greater than in any other species (Tables 13 and 16).

The second ceratobranchial is an unossified, slightly curved rod of cartilage articulating at its proximal end with the tip of the first basibranchial and with the anterior end of the epibranchial at its distal end.

The ceratohyal was ossified in one specimen and unossified in the other two. In the specimen with ossification, this amounted to 11 percent of the total volume (Table 1). Only in A. mabeei, A. t. melanostictum, and Rhyacotriton is the ratio of ceratohyal length to total hyobranchial skeleton length greater than in this species (Table 19).

The lateral arms of the second basibranchial are longer than the anterior arm, and the former contain cartilage on their tips. The average ossification is 76 percent.

The ratio of mandible length to mandible width is much smaller than in other species (Table 14), indicating a short mandible.

MUSCULATURE (Fig. 10)

Intermandibularis posterior originates along the dorsomedial margin of each mandibular ramus. The fibers extend transversely and slightly posteriorly to attach to the fascia of the linea alba. It covers more than three-quarters of the area between the rami of the mandible. The anterior portion at the point of the chin is missing, and the genioglossus can be seen in that position.

Interhyoideus posterior originates from fascia which attaches to the posterior tip of the mandible, the quadrate, the squamosal, and the otic capsule. The posterior fibers originate in the fascia cephalodorsalis. The origin overlaps the insertion of the depressor mandibulae on the tip of the mandible. The insertion is into the midventral raphe. The anterior fibers blend in with those of the interossaquadrata.

Depressor mandibulae originates along the dorsal end of the squamosal, the ventral and posterior surfaces of the otic capsule, and along the fascia cephalodorsalis, the fibers of this muscle converge onto the posterior tip of the mandible where they insert as a short, stout tendon. There are also a few short fibers which extend from the ventral surface of the quadrate to the posterior tip of the mandible.

Levator mandibulae corresponds closely to the description that is given in the section on general musculature. There is considerable intermingling of fibers between the levator mandibulae posterior and the levator mandibulae externus.

Interossaquadrata is a fan-shaped muscle which originates from the ventral surface of the quadrate anterior to the hyoquadrate ligament, from the articulation of the ceratohyal and the quadrate, and from the ventral surface of the posterior tip of the ceratohyal. The anterior fibers, arising from the quadrate, lie dorsal to the posterior fibers and are directed in an anteromedial direction. The posterior fibers, which arise from the ceratohyal tip, extend transversely and slightly posteriorly. The fibers form a delicate fan which adheres to the dorsal surface of the intermandibularis posterior and blends in well with the subhyoideus. The insertion is into the fascia of the dorsal surface of the intermandibularis posterior.

Subhyoideus originates from the ventral surface of the posterior tip of the ceratohyal immediately medial to the origin of the interossaquadrata and the insertion blends in with the latter before inserting into the dorsal fascia of the intermandibularis posterior.

Geniohyoideus originates from a line on the posterior edge of the mandible beginning at the symphysis and extending laterally about 1.5 mm. The fibers extend directly caudad to form two bands of muscle lying side by side along the venter of the throat. The thin fascia of the linea alba overlaps this muscle ventrally. The insertion is onto the second basibranchial cartilage and the tendonous inscription that extends laterally from the arms of the second basibranchial.

Genioglossus has two parts. The ventral portion originates along a line on the posterior edge

of the mandible. The line in this case lies immediately ventral to the origin of the geniohyoideus and extends from the symphysis to a point about 2.0 mm lateral to the symphysis. The fibers extend caudomesially to insert into the aponeurosis lingualis and onto the otoglossal. This is a large muscle in this species and is thicker and broader than in the other species investigated.

The origin of the dorsal portion of the genioglossus is from a line along the mandible immediately dorsal to the origin of the geniohyoideus. The fibers spread out as they pass distally over the throat and become almost indistinguishable from the fascia of the floor of the mouth. It is into this fascia that these fibers finally insert at a position lateral to the second radial cartilage. The tip of the first radial is overlapped by the fibers of this muscle, and the medial fibers also attach to the posterior edge of the tip of the second radial cartilage as the latter turns dorsad to articulate with the end of the otoglossal.

Subarcualis rectus I attaches at its origin to the dorsal edge of the posterior tip of the epibranchial. The fibers wrap around and enclose the epibranchial and the lateral portion of the ceratobranchial in a sheath. There is an opening in the sheath which faces medially and into which the second ceratobranchial passes on its way to articulate with the epibranchial. The fibers lie parallel with the ceratohyal and spread out over the latter's anterior expanded end. The insertion is along the anterior margin of the ceratohyal.

Rectus cervicis superficialis originates along the lateral margin of the dorsal surface of the sternum and along the transverse tendonous inscription which separates it from the rectus abdominus. It passes forward as a thin, broad band to the level of the second basibranchial, which is partially imbedded in this muscle. The portion of this muscle up to this point has only two tendonous inscriptions crossing it. The portion running anterior from the second basibranchial is thicker and narrower than the posterior portion. This anterior portion inserts onto the posterior edge of the medial end of the first ceratobranchial.

Rectus cervicis profundus is a direct forward continuation of the rectus abdominus, arising at the level of the sternum and passing forward alongside of the pericardium and both dorsal and lateral to the rectus cervicis superficialis. At the level of the second basibranchial, it is directly dorsal to the rectus cervicis superficialis. It continues forward from this point to lie in a posi-

tion dorsal to the first basibranchial and the hyoglossus. The two rectus cervicis profundus muscles together are about as wide as the first basibranchial. This muscle inserts on the posterior edge of the otoglossal.

Hebosteoypsiloideus is a narrow muscle which arises from the dorsal surface of one of the myosepta of the rectus cervicis profundus. In *Ambystoma talpoideum*, this muscle originates from the second myoseptum posterior to the second basibranchial. The fibers extend forward dorsal to the rectus cervicis profundus and then cross the rectus cervicis superficialis to attach to the dorsal surface of the anterior arm of the second basibranchial.

Hyoglossus is a thick, well-developed muscle which originates from the dorsal surface of the base of the first radial and the adjacent surface of the first basibranchial. The insertion is laterad along the tip of the second radial.

MARBLED SALAMANDER.

Ambystoma opacum (Gravenhorst)

Salamandra opaca Gravenhorst, Vergl. Uebers. Zool. Syst., 1807, p. 421.

The geographical range extends along the Atlantic Coast of the United States from Massachusetts to Florida and westward to Texas, Arkansas, Missouri, Indiana, Illinois, and Wisconsin. This species is found in drier habitats than most of the other species of the genus. It is often collected in sandy areas bordering ponds and slow-moving streams. The females are slightly larger than the males, the total length ranging up to 120 mm. The ground color is black and is interrupted by light markings in the form of transverse bands. These bands are narrow dorsally and widen as they approach the upper sides of the body, where they may unite with the ends of adjacent bands to enclose a series of regular black spots along the midline of the back. Males have bright white transverse bands, while those of the females are grayish in color. The body is thick, short, and cylinder shaped. The gular fold is prominent, and there are 12 costal grooves if the one immediately above the foreleg is counted. The vomerine teeth form a transverse line which is interrupted both at the midline and at a point just back of the internal nares. Most species of this genus deposit their eggs in the springtime in ponds or slow-moving streams. The Marbled Salamander, however, deposits its eggs in the fall under logs, pieces of bark, or other materials on the surface of the ground. These laying sites are subsequently flooded by the last summer or fall rains.

HYOBRANCHIAL SKELETON (Fig. 11)

The average amount of bone in the first basibranchial for the four specimens was 41 percent. The basibranchial-radial articulations are seen as definite lines. When the length of the first basibranchial is compared with the total length of the hyobranchial apparatus or with the length of the first ceratobranchial, it is seen to be greater than in any of the other species (Tables 4 and 5).

The first radials do not connect with the anterior tip of the ceratohyals. The radials are wholly cartilaginous and are intermediate in length between the extremes seen in other members of the family.

The second radials are directed in a dorsolateral direction while gradually tapering to a fine point which articulates with the otoglossal. The otoglossal is arched dorsally into the tongue and is entirely cartilaginous.

The boneless first ceratobranchial forms a smooth arch that continues with the epibranchial to form a quarter circle of cartilage.

The second ceratobranchial is a thin cartilaginous rod only slightly curved and articulating on the epibranchial well posterior to the first ceratobranchial-epibranchial articulation.

The ceratohyal is unossified except in two specimens, in which a small ossification center is found in the posterior tip of each of these structures.

The second basibranchial is unossified except in one specimen, and is shaped as an inverted V.

MUSCULATURE (Fig. 11)

Intermandibularis posterior originates along the dorsomedial edge of the rami of the mandible and passes transversely over the venter of the throat to insert into the linea alba. There is no subdivision of this muscle into parts. The ventral portion of the genioglossus can be seen in the angle of the chin inasmuch as the intermandibularis posterior does not completely cover the intermandibular space at that point. The posterior fibers extend slightly caudad and overlap the interossaquadrata.

Interhyoideus posterior originates from the fascia which is attached to the lateral aspect of the tip of the mandible, the quadrate, the squamosal, the otic capsule, and from fibers which attach to the fascia cephalodorsalis. The fibers spread out as they move distally and medially until they form a thin sheet which inserts into the skin of the gular fold and the midline fascia. The anteriormost fibers are blended with those of the interossaquadrata near their insertion.

Depressor mandibulae originates from the squamosal bone of the skull, attaching along its entire posterolateral surface except for the ventral 1 to 2 mm. It also arises from the fascia cephalodorsalis and the lateral surface of the otic capsule. It inserts onto the posterior tip of the mandible.

Levator mandibulae is essentially the same in its origins and insertions as that description which has been given previously in the section on general musculature.

Interossaquadrata originates on the posterior surface of the quadrate and from the ventral surface of the articulation between the quadrate and the tip of the ceratohyal. A few fibers also arise from the posterior tip of the mandible. The anterior fibers extend anteromedially, while the posterior ones are in a posteromedial direction. It inserts into the midventral raphe of the throat. This is a thin, fan-shaped muscle.

Subhyoideus originates along the anteroventral edge of the posterior end of the ceratohyal and then fans out slightly as it proceeds forward over the throat. It lies ventral to the subarcualis rectus I and inserts into the dorsal fascia of the intermandibularis posterior. The latter covers the anterior portion of this muscle ventrally. The insertion end is displaced slightly lateral from the subarcualis rectus I.

Geniohyoideus originates from the posterior edge of the mandible along a line which begins about 1.5 mm lateral to the symphysis and extends laterally about 1.0 mm. The anteromedial end of this muscle is overlapped ventrally by the ventral portion of the genioglossus. The lateral fibers extend directly caudad, while the medial fibers are in a mediocaudal direction for a short distance before continuing directly caudad. The insertion is onto the second basibranchial cartilage, with the lateral fibers attaching into the tendonous inscription of the rectus cervicis superficialis.

Genioglossus has a ventral portion which originates from the ventral and posterior surfaces of the mandible beginning at the symphysis and extending laterally about 2 to 3 mm. From this area of origin, the fibers extend caudomedially to form a small triangle which overlaps the anteromedial end of the geniohyoideus. This ventral portion is divided into two portions by a separation in the fibers. It inserts into the aponeurosis lingualis. A few fibers continue along in this ligament to attach to the first basibranchial and to the otoglossal.

The dorsal portion of the genioglossus originates along the posterior edge of the mandible

from the symphysis to a point about 1.5 mm lateral from the symphysis. The medial fibers insert onto the posterior edge of the lateral half of the second radial, while the lateral fibers extend beyond this point and attach into the fascia, forming the floor of the mouth.

Subarcualis rectus I originates on the dorsal edge of the tip of the epibranchial. The fibers wrap around and enclose this end of the epibranchial in a sheath and extend forward parallel with the ceratohyal. After spreading out over the ceratohyal's expanded anterior end, these fibers insert along the ventral edge of the anterior margin of this cartilage.

Rectus cervicis superficialis originates from the dorsal surface of the lateral half of the sternum. Lateral fibers originate on the tendonous inscription which separates this muscle from the rectus abdominus. After passing forward from the second basibranchial, the medial fibers insert onto the posterior end of the first basibranchial, whereas the lateral fibers insert onto the posterior surface of the medial end of the first ceratobranchial.

Rectus cervicis profundus constitutes a direct forward continuation of the rectus abdominus, arising at the level of the sternum. It is situated in a dorsolateral position with respect to the rectus cervicis superficialis. The fibers pass ventral to the second ceratobranchial and dorsal to the first ceratobranchial. It continues forward dorsal to the first basibranchial and the hyoglossus to insert onto the posterior edge of the otoglossal.

Hebosteoypsiloideus is a narrow muscle which originates from a more posterior position than in most of the other species. It arises from the third tendonous inscription posterior to the second basibranchial and extends anteriorly and then medially to insert onto the dorsal aspect of the second basibranchial.

Hyoglossus originates from the aponeurosis lingualis and the lateral edge of the dorsal surface of the anterior end of the first basibranchial. The fibers converge toward the insertion to form a small, triangular-shaped muscle that attaches laterally to the posterolateral edge of the second radial cartilage as the latter curves dorsad to join the end of the otoglossal. There are also a few fibers which extend laterally to attach to the fascia at the base of the tongue.

TEXAS SALAMANDER.

Ambystoma texanum (Matthes)

Salamandra texana Matthes, Allg. deutsche naturh, Zeitschr., N. S. Vol. I, 1855, p. 266.

The Texas Salamander is dark brown in color with grayish, irregular, lichenlike blotches. Total length may reach 153 mm. A slender head and small mouth are characteristic of this species. The vomerine teeth are very slender and are arranged in a transverse line that is entirely between the internal nares and is interrupted at the midline. There are usually 14 costal grooves. It is found in Iowa, Ohio, Indiana, and Illinois in the north and westward to Nebraska and Kansas. It extends southward to Texas and Louisiana and has also been reported from North and South Carolina, Tennessee, Kentucky, and West Virginia.

HYOBRANCHIAL SKELETON (Fig. 12)

The first basibranchial is a shield-shaped structure with a large core of bone averaging 38 percent of the total volume (Table I). The lines of articulation with the radials are distinct. The first basibranchial is situated posteriorly as compared to its position in most of the other species. Only in *A. annulatum, A. cingulatum, A. mabeei,* and *Rhyacotriton* is the first basibranchial in a more posterior position (Table 12). This structure is wider in this species in relation to its length than in any of the others, except *A. cingulatum* (Table 15).

The first radials are long and curved, and they are attached to the tips of the ceratohyals by a short ligament. Their length in relation to the first basibranchial is exceeded only by *Rhyacotriton, A. mabeei* and *Dicamptodon* (Table 6).

The bases of the second radials overlap the medial end of the first ceratobranchial ventrally. These radials are also without ossification. They articulate with the tips of the otoglossal, a dorsally curved rod of cartilage.

The first ceratobranchial is cartilage. It is a gradually curved rod whose medial end is fused to the first basibranchial.

The epibranchial is devoid of bone and moderate in length (Table 16).

The second ceratobranchial is longer than the first ceratobranchial and, in fact, the ratio of the length of the second ceratobranchial (the second branchial arch) to the length of the first branchial arch (the first ceratobranchial plus the epibranchial) is greater than in the others except *A. annulatum* and *A. cingulatum* (Table 17). The second ceratobranchial is entirely cartilaginous.

In three of the five specimens, the ceratohyals contained ossification centers in the posterior tips. The other specimens were unossified in the ceratohyals. This lack of consistency in ossification between these five specimens cannot be at-

tributed to size differences since they were all approximately equal in this respect. There may have been an age difference between the five specimens, although they all were collected on the same day and in the same location, and all five were completely transformed adults.

The second basibranchial is shaped like an inverted V and contains cartilage on the two tips. The average ossification is 65.1 percent.

MUSCULATURE (Fig. 12)

Intermandibularis posterior originates along the dorsomedial edge of the mandible. The fibers extend transversely to insert into a broad midline of fascia, the linea alba of the throat. A small area is opened at the point of the chin through which the ventral portion of the genioglossus can be seen. The posterior portion of the intermandibularis posterior overlaps the anterior end of the interossaquadrata ventrally.

Interhyoideus posterior is attached at its origin to several bony and fascial surfaces, arising from the posterior tip of the mandible, the lateral surface of the quadrate, the lateral surface of the squamosal, and from the fascia cephalodorsalis. It inserts into the gular fold and into the median ventral raphe which is a posterior continuation of the fascial material into which the intermandibularis posterior and the interossaquadrata insert.

Depressor mandibulae originates along the upper squamosal, the ventral and posterior surfaces of the otic capsule, and posteriorly from the fascia cephalodorsalis. The fibers of this muscle insert onto the posterior tip of the mandible where they function to depress or lower the mandible.

Levator mandibulae in *Ambystoma texanum* is essentially the same as the description given previously in the section on general musculature.

Interossaquadrata originates along the ventral surface of the articulation between the ceratohyal and the quadrate. The insertion is into the dorsal side of the median fascia into which the intermandibularis posterior inserts. The fibers extend medially to a point somewhat short of the midline and, consequently, this muscle overlaps ventrally the lateral half of the geniohyoideus.

Subhyoideus originates along the anteroventral edge of the posterior end of the ceratohyal. It extends dorsal to the interossaquadrata at its origin end. The fibers are directed more medially in this species than in most of the others, and consequently the insertion end overlaps the venter of the subarcualis rectus 1 medially rather

than laterally. It fans out to insert into the dorsal fascia of the intermandibularis posterior.

Geniohyoideus originates on the posterior surface of the mandible. More precisely, the origin is along a line extending laterally from the mandibular symphysis for a distance of 1.5 to 2.0 mm. The fibers run caudad to insert onto the second basibranchial and into the tendonous inscription of the rectus cervicis superficialis that extends laterally at that point.

Genioglossus has a ventral portion which originates along the posterior edge of the mandible immediately ventral to the medial portion of the origin of the geniohyoideus. The fibers extend caudomedially and overlap the medial anterior end of the geniohyoideus. They insert into the aponeurosis lingualis at about the level of the anterior edges of the ceratohyals, and a few fibers continue in the aponeurosis lingualis to the first basibranchial and to the otoglossal.

The dorsal portion originates along the same line on the mandible as the ventral portion, but the fibers extend caudolaterally. The medial fibers are dorsal to the geniohyoideus, and they insert onto the anterior edge of the second radial near its tip. The lateral fibers insert into the fascia of the tongue at its base and contribute to the floor of the mouth.

Subarcualis rectus 1 originates on the dorsal side of the posterior tip of the epibranchial, from which the fibers proceed forward, wrapping around and enclosing the epibranchial in a sheath of muscle. These fibers continue forward parallel with the ceratohyal to insert onto the latter's expanded anterior end along the anterior margin.

Rectus cervicis superficialis originates on the dorsal surface of the posterior end of the sternum. The fibers extend dorsal to the anterior part of the scapula and dorsal to the coracoids. It lies on the ventral surface of the pericardium. These fibers insert onto the medial end of the first ceratobranchial just before the latter articulates with the first basibranchial. It also inserts onto the point of articulation of these two cartilages and onto the posterior tip of the first basibranchial. The medial three-fourths of this muscle also attaches to the second basibranchial.

Rectus cervicis profundus passes forward alongside the pericardium and is both dorsal and lateral to the rectus cervicis superficialis. It continues forward through the opening formed by the two ceratobranchial cartilages and finally inserts onto the posterior edge of the otoglossal.

Hebosteoypsiloideus originates from the dorsal surface of a myoseptum of the rectus cervicis profundus. The particular myoseptum in this case is the second one posterior to the second

basibranchial. This narrow muscle extends forward dorsal to the rectus cervicis profundus. At the level of the second basibranchial, it turns medially and crosses the rectus cervicis superficialis to attach along the dorsal surface of the second basibranchial.

Hyoglossus is a small muscle situated between the first basibranchial ventrally and the rectus cervicis profundus dorsally. It originates from the dorsal surface of the anterior end of the first basibranchial and along the lateral margin of the dorsal surface of this cartilage. From this point, the fibers extend caudolaterally to wrap around and insert onto the posterolateral edge of the tip of the second radial cartilage. There are also a few fibers which continue for a short distance into the sides of the base of the tongue.

Chihuahua Salamander.

Ambystoma rosaceum Taylor

Ambystoma rosaceum Taylor, Copeia 1941 (3): 143-144, figs. 1a and 1b.

This species has a uniform dark brown ground color with a lighter brown ventrally. Along the chin and tail there are light, indistinct spots which may also continue along the sides of the body in a somewhat linear pattern. There are usually 11 costal grooves, counting one each in the axilla and groin. Vomerine teeth are divided into two groups of 26 each, separated by a midline diastema. The tail is compressed laterally and has a small dorsal tail fin. There are glands scattered over the body, becoming prominent along the proximal third of the dorsal ridge of the tail and also forming a parotid gland. These glandular areas are similar to but not as well developed as in *A. gracile*. Total length may reach 165 mm. These salamanders are found in the mountains of the Sierra Madre Occidental from El Salto, Durango, to northern Chihuahua and northeastern Sonora.

Hyobranchial Skeleton (Fig. 13)

The first basibranchial is shield-shaped when viewed from the ventral aspect. In cross section, it is a flat oval. The core of this structure is bone, constituting an average of 28 percent of the total volume (Table 1). The articulation lines separating this structure from the radials are distinct. The first basibranchial is situated anteriorly with respect to the position of the mandible. Only *A. t. nebulosum* has a more anteriorly situated first basibranchial (Table 12).

The first radials are sharply curved laterally and entirely cartilaginous. They are long, as indicated by the fact that the ratio—radial I length to basibranchial I length—is greater in this species than in the others, with the exception of *A. mabeei*, *A. texanum*, *Rhyacotriton*, and *Dicamptodon* (Table 6).

The second radials are bent in a slightly posterior direction when in a resting position. They are wholly cartilaginous and attach to the ends of the annular otoglossal.

No bone is found in the first ceratobranchial, and they are rather straight, the major curve in the first branchial arch occurring at the anterior end of the epibranchial.

In one of the three available specimens, the epibranchials and ceratohyals were devoid of bone in their posterior tips. The other two specimens had well-developed ossification centers in these structures. The average ossification for the three specimens was 36 percent for the epibranchials and 4.8 percent for the ceratohyals.

The ratio of ceratohyal width to ceratohyal length is equalled in *A. t. melanostictum* and exceeded in all of the others (Table 14).

The totally cartilaginous second ceratobranchial is long when analyzed by the ratio of length of second ceratobranchial to length of first ceratobranchial (Table 8).

The lateral arms of the second basibranchial contain cartilage on their tips, the cartilage constituting an average of 31 percent of the total volume (Table 1).

The mandible length compared to the mandible width is a rather high ratio in this species, being exceeded only by four others—*Dicamptodon*, *A. annulatum*, *A. mabeei*, *A. maculatum*, and *A. cingulatum* (Table 9).

Musculature (Fig. 13)

Intermandibularis posterior originates on the dorsomedial surface of the mandible and extends medially to the linea alba. It is seen immediately under the skin of the throat and overlaps the more dorsally situated interossaquadrata and subhyoideus muscles. The posterior fibers are directed obliquely caudomediad, while the majority of the fibers are transverse.

Interhyoideus posterior originates from fascia which is in turn attached at several points, the lateral aspect of the posterior tip of the mandible, the quadrate, the squamosal, the otic capsule and the fascia cephalodorsalis. The fibers spread out as they extend in a caudomesial direction to insert into the gular fold and the midventral fascia.

Depressor mandibulae originates on the dorsal end of the squamosal, the ventral and posterior surfaces of the ear capsule and along the

fascia cephalodorsalis. It inserts onto the posterior tip of the mandible.

Levator mandibulae is essentially the same as the description which is given in the earlier section on general musculature.

Interossaquadrata originates on the ventral surface of the quadrate, anterior to the hyoquadrate ligament and from the hyoquadrate ligament itself. This is a delicate muscle which is easily lifted along with the intermandibularis posterior. It is fan-shaped, the anterior fibers lying in an anteromesial direction and the posterior fibers in a posteromesial position. It inserts into the median raphe into which the intermandibularis posterior and the interhyoideus posterior also insert.

Subhyoideus originates from the ventrolateral margin of the posterior end of the ceratohyal. The posterior fibers of this thin muscle blend in with those of the interossaquadrata, making separation of these two muscles difficult at their insertion ends. This is also a delicate muscle that is easily disrupted when the intermandibularis posterior is lifted. The insertion end overlaps laterally part of the ventral surface of the subarcualis rectus I. It inserts into the dorsal surface of the fascia of the intermandibularis posterior.

Geniohyoideus originates from a short line on the posterior surface of the mandible. This line runs laterally for about 3.0 mm from a point about 1.5 mm lateral to the symphysis. The fibers extend caudad to form a band of muscle which inserts onto the second basibranchial and onto the tendonous inscription lateral to the second basibranchial. This muscle appears to be rather narrow in this species.

Genioglossus originates along a line beginning at the mandibular symphysis and extends laterally about 2.0 mm along the posterior surface of the mandible. The fibers extend caudomesiad to form a small triangle. The insertion is into the aponeurosis lingualis, and a few fibers continue on to the anterior edge of the first basibranchial. A few fibers also attach to the otoglossal cartilage.

The broader lateral portion originates immediately dorsal to the origin of the ventral portion but extends laterally from the symphysis for a distance of 3 to 4 mm. The fibers fan out and extend posterolaterally to insert into the fascia of the floor of the mouth at about the level of the second radial tip.

Subarcualis rectus I originates along the dorsal edge of the posterior end of the epibranchial, wraps around this cartilage, and extends forward over the ventral surface of the ceratohyal. The fibers fan out and insert along the anterior margin of this cartilage.

Rectus cervicis superficialis originates on the dorsal surface of the sternum and the tendonous inscription extending laterally from the sternum. It extends dorsal to the coracoid cartilages and ventral to the pericardium. The second basibranchial is partially enveloped by this muscle as it continues anteriorly. It then becomes narrower and thicker and turns medially to insert onto the posterior tip of the first basibranchial and onto the posterior edge of the medial end of the first ceratobranchial.

Rectus cervicis profundus appears at the level of the sternum as a flat band extending forward alongside and dorsal to the rectus cervicis superficialis. At the level of the omohyoideus, it begins to turn medially. Forward from the second basibranchial, it is a thick, narrow band which lies dorsal to the rectus cervicis superficialis. The fibers pass ventral to the second ceratobranchial and dorsal to the first ceratobranchial. From this point forward, it leaves the rectus cervicis superficialis and inserts onto the posterior edge of the otoglossal.

Hebosteoypsiloideus originates from one of the myosepta of the rectus cervicis profundus. The particular myoseptum is the second one posterior to the second basibranchial. It is a narrow muscle which at first extends directly forward dorsal to the rectus cervicis profundus. After a short distance, it turns across the dorsal surface of the rectus cervicis superficialis and inserts onto the dorsum of the second basibranchial.

Hyoglossus is a small muscle extending from the first basibranchial to the tip of the second radial. It is triangular in shape, with the base of the triangle situated along the dorsal surface of the anterior end of the first basibranchial and along the lateral margin of this cartilage to the base of the second radial. The point of the triangle is the insertion end which attaches onto the tip of the second radial and out into the adjoining fascia.

<div align="center">

TIGER SALAMANDER.

Ambystoma trigrinum Green

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Salamandra tigrina Green, 1825, Jour. Acad. Nat. Sci. Phil., (1), 5:116.

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EASTERN TIGER SALAMANDER.

Ambystoma tigrinum tigrinum (Green)

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Salamandra tigrina Green, Journ. Ac. Nat. Sci. Phila., Vol. 5, 1825, p. 116.

This subspecies ranges extensively throughout most of the United States, from New York to northern Florida and westward to Texas in the south and Minnesota and parts of Ontario in the north. It is a burrower and spends most of the year underground. Its burrowing habit is abandoned only during the breeding season, during which time it can be found in ponds and slow streams. This is the largest species of the genus *Ambystoma*, attaining a length of 254 mm in some individuals. It is a stout-bodied salamander with 12 costal grooves when those in the axilla and groin are counted. The gular fold is prominent, and the vomerine teeth are usually in a continuous series, although there is occasionally a break in this series at the midline. Males are usually larger than females, and the tail and hind legs are also usually longer in male specimens. Ground color is dark brown or dull black. The venter is olive yellow in color. Brownish olive or brownish yellow blotches are scattered over the dark ground color. These blotches may fuse somewhat between the costal grooves to form short bands along the sides of the trunk.

Northwestern Tiger Salamander.

Ambystoma tigrinum melanostictum (Baird)

Siredon lichenoides melanostictum Baird, 1860 Expl. Surv. R. R. Miss. Pacific, 12, pt. 2, p. 306.

This subspecies is characterized by extreme development of the light colored areas of the skin. These areas converge greatly such that the darker ground color persists as irregular patches. The light areas are pale yellow and the ground color is brown to black. There are usually 13 costal grooves when one in the axilla and two that converge in the groin are counted. There may be three series of vomerine teeth which form a forward arching line in front of the internal nares; however, the central series is occasionally interrupted at the midline. Adults may reach a total length of 219 mm. Adult specimens are sometimes found in damp situations under logs or stones; whereas, during the breeding season, they may be abundant in the mountain lakes and ponds throughout their range. They are found in British Columbia, Alberta, Washington, Oregon, Idaho, Montana, Wyoming, North Dakota, South Dakota, and Nebraska.

Clouded Tiger Salamander.

Ambystoma tigrinum nebulosum Hallowell

Ambystoma nebulosum Hallowell, Proc. Acad. Nat. Sci. Phila., 6, p. 209.

This subspecies of tiger salamander is characterized by having black spots on a dark ground color of olive green or dark gray. It has a well developed gular fold and usually 13 costal grooves when the one in the axilla and the two that run together in the groin are counted. The line formed by the vomerine teeth tends to arch forward between the internal nares and may or may not form a continuous series. When not continuous, the tooth line will be interrupted just medial to the inner margin of the naris and also at the midline. Males tend to be slightly larger than females. Total length may reach 230 mm. During the breeding season the swollen vent is characteristic of the male. These salamanders are found commonly in the mountain lakes and ponds and also occasionally beneath logs and stones. Their range extends over western Colorado, northwestern New Mexico, northern Arizona, the inner basin of Utah, and the Colorado Plateau in Utah.

The anatomical descriptions which follow are based upon a study of the above three subspecies of Tiger Salamander.

Hyobranchial Skeleton (Fig. 14-16)

The first basibranchial is shield shaped and has a central core of bone. The percentages of ossification of the first basibranchial are similar for *A. t. melanostictum* and *A. t. tigrinum* (Table 1).

The relative position of the first basibranchial along the anteroposterior axis of the throat is very similar for these three subspecies and, as a group, their first basibranchials are more anterior than they are in the other species (Table 12).

The first radials attach to the tips of the ceratohyals by a short ligament. These radials are moderate in length and unossified.

The second radials also contain no bone and are curved dorsally where their distal ends articulate with the ends of the otoglossal. The otoglossal is unossified and arched dorsally into the tongue.

The first ceratobranchials are entirely cartilaginous and moderate in length. They are uniform in width and thickness throughout their length and are flattened dorsoventrally.

The epibranchials were ossified in all 10 of the specimens examined. The amount of ossification was notably different, however, in *A. t. nebulosum* from that found in the other two subspecies (Table 1). This, however, is based on a limited number of specimens.

The average first ceratobranchial length, when compared to the length of the epibran-

chial, was shorter for *A. t. melanostictum* and *A. t. nebulosum* than all of the others except *A. talpoideum* (Table 13).

The second ceratobranchial compared to the first ceratobranchial has a smaller ratio in the *tigrinum*-group than in other species except for *Dicamptodon* and *Rhyacotriton* (Table 8).

Two of the subspecies were found to have ossification centers in the ceratohyal tips. The third, *A. t. melanostictum*, has no bone in the ceratohyals. The average percent ossification of the ceratohyals in *A. t. nebulosum* and *A. t. tigrinum* was 8 and 5 respectively (Table 1). The ceratohyal length in relation to the total length of the hyobranchium is shorter in *A. t. tigrinum* than in the other two tiger salamander subspecies (Table 19). This ratio is moderate for the *tigrinum* group as a whole.

The second basibranchial in the *tigrinum* group is triradiate in shape, with the anterior arm being considerably shorter than the lateral arms. The anteroposterior length of this element is greater in *A. t. tigrinum* in relation to the side-to-side length than in the other two subspecies (Table 18). This ratio is also moderate compared with all the other species.

As a group, the *tigrinum* subspecies have a broad head compared with the other species. The ratio—mandible length to mandible width— is smaller in *A. tigrinum* than in the others except for the mole salamander, *A. talpoideum* (Table 9).

MUSCULATURE (Fig. 14-16)

Intermandibularis posterior originates on the dorsomedial surface of the mandible. The direction of the fibers is transverse for the most part, except for the posterior fibers which are directed caudomedially. It inserts into the linea alba of the throat.

Interhyoideus posterior originates from fascia which is attached to the lateral part of the posterior tip of the mandible, the quadrate, the squamosal, and the otic capsule, with some posterior fibers originating from the fascia cephalodorsalis. It inserts into the skin and fascia of the gular fold and into the midventral line. The anterior fibers blend imperceptibly with those of the interossaquadrata. The posterior edge of this muscle (the gular fold) is more anteriorly situated in *A. t. nebulosum* than in any of the other specimens included in this study (Table 11).

Depressor mandibulae attaches along the dorsal end of the squamosal, the ventral and posterior surfaces of the otic capsule, and in the fascia cephalodorsalis. The insertion is onto the posterior tip of the mandible.

Levator mandibulae is essentially the same as the description given in the earlier section on general musculature.

Interossaquadrata originates from the ventral surface of the quadrate anterior to the hyoquadrate ligament and from the ligament itself. The anterior fibers extend anteromediad and ventral to the subarcualis rectus I, whereas the posterior fibers lie parallel with those of the interhyoideus posterior. The insertion is in the median raphe into which the intermandibularis posterior and interhyoideus posterior also insert.

Subhyoideus originates on the ventrolateral margin of the posterior 2 to 3 mm of the ceratohyal. It is a thin muscle, the posterior fibers of which blend in closely with those of the interossaquadrata. The fibers lie parallel with the subarcualis rectus I; and, in fact, if the intermandibularis posterior is removed carefully, the subhyoideus can be seen lying against the ventral surface of the subarcualis rectus I. The insertion end overlaps the venter of the subarcualis rectus I laterally. This muscle inserts into the dorsal fascia of the intermandibularis posterior.

Geniohyoideus originates from a short line along the posterior surface of the mandible. This line begins at a point about 1.5 mm lateral to the symphysis and extends laterally about 3.0 mm. The fibers pass caudad and slightly mediad to insert onto the second basibranchial. A few of the lateral fibers also insert onto the tendonous inscription of the rectus cervicis superficialis that extends laterally from the arms of the second basibranchial.

Genioglossus has a ventral portion which originates along a line beginning at the mandibular symphysis and extending laterally about 2.0 mm. The fibers extend caudomedially and form a small triangle that is seen between the anterior ends of the geniohyoideus. The insertion is into the aponeurosis lingualis which connects the root of the tongue with the first basibranchial and with the otoglossal.

The lateral portion is a broader muscle which originates along a line immediately dorsal to the origin of the ventral portion but extends laterally from the symphysis for a distance of 3 to 4 mm. These fibers extend posterolaterally to insert into the base of the tongue. The medial fibers attach to the tips of the second radials.

Subarcualis rectus I originates from the dorsal side of the posterior end of the epibranchial cartilage. The fibers radiate around and enclose this end of the epibranchial, forming a sheath at the posterior end of the muscle with the opening of the sheath facing medially and into which the ceratobranchial passes. The fibers lie parallel with the cartilage and insert on the ventroante-

rior border of the expanded anterior end of the ceratohyal.

Rectus cervicis superficialis originates from the posterior two-thirds of the dorsal surface of the sternum. The fibers of this muscle extend forward dorsal to the sternum, dorsal to the coracoids, and ventral to the pericardium to insert onto the dorsal surface of the second basibranchial and into the tendonous inscription from which the geniohyoideus arises. The part anterior to the second basibranchial inserts onto the posterior tip of the first basibranchial and the posterior edge of the medial end of the first ceratobranchial cartilage.

Rectus cervicis profundus is a direct forward continuation of the rectus abdominus. At the level of the sternum, it passes forward along the side of the pericardium and both dorsal and lateral to the rectus cervicis superficialis. It is ventral to the second ceratobranchial and dorsal to the first ceratobranchial and inserts finally on

the posterior edge of the otoglossal cartilage.

Hebosteoypsiloideus is a narrow muscle originating from the dorsal surface of one of the myosepta of the rectus cervicis profundus. In this species it arises from the second myoseptum posterior to the second basibranchial, extends dorsal to the rectus cervicis profundus, turns medially for a short distance dorsal to the rectus cervicis superficialis, and inserts on the dorsal surface of the second basibranchial.

Hyoglossus is a small muscle which lies ventral to the rectus cervicis profundus and originates from the dorsal surface of the anterior end of the first basibranchial cartilage and along the lateral margin of the dorsal surface of this cartilage. The fibers extend caudolaterally to wrap around the tip of the second radial cartilage. The point of insertion is on the posterolateral edge of the second radial, although a few of the posterior fibers extend laterally to insert into the sides of the base of the tongue.

DISCUSSION

The foregoing descriptions of comparative morphology have been condensed to 48 characters which we have used in a cluster analysis using the method of Wishart (1969). We believe that the use of this method, together with the methods of descriptive morphology, provides for an analysis of the data which is more precise than is possible by use of descriptive morphology alone.

A character analysis produced by statistical methods concerning relationships between the various species of the Ambystomidae provides useful information for the deduction of a phylogeny. It must be kept in mind, however, that the basis for these relationships, as used in this study, is comparative morphology of the hyobranchium and throat musculature. It is entirely possible that these results could be different using information derived from different sources, such as the skull or external morphology.

It is not known whether the individual characters are evolving as independent units or whether they are parts of larger integrated systems. We suspect that some are related to the development of the feeding and/or breathing mechanisms.

The characters used in the cluster analysis are of two types—numeric and binary. The former are recorded as the length of a particular structure, the ratio of lengths of two different structures, or as a percentage of ossification of a structure. Binary characters are expressed as

either the presence or absence of a particular structure, and are recorded in the data as 0 or 1 for absence and presence, respectively.

The numbered paragraphs which follow contain explanations of each of the 48 characters. Some of the binary characters contain two or three different attributes so that the total number of attributes amounts to 63 (22 numeric and 41 binary). The number of each paragraph corresponds to the character and/or attribute number. (See Tables 2 and 3 for the specific characters for each individual.)

1. The ratio of the distance between the mental symphysis and the posterior edge of the intermandibularis posterior to the distance between the mental symphysis and the anterior edge of the pectoralis.

2. The ratio of the distance between the mental symphysis and the gular fold to the distance between the mental symphysis and the anterior edge of the pectoralis.

3. The ratio of mandible length to mandible width.

4. The ratio of the distance between the mental symphysis and the anterior edge of the first basibranchial to the length of the mandible.

5. This ratio is a comparison of the length of the first basibranchial with the total length of the hyobranchial apparatus. The basibran-

chial length is taken as the distance between the anterior edge of the first basibranchial and a line drawn between the posterior edges of the medial ends of the first two cerato-branchials. The latter point was chosen rather than the extreme posterior tip of the first basibranchial because the articulation between the first basibranchial and the second ceratobranchial was often indistinct.

6. The ratio of the length of the first basi-branchial to the length of the first cerato-branchial.

7. The ratio of the length of the first basi-branchial to the total length of the first bran-chial arch.

8. This ratio compares the width of the first basibranchial to its length.

9. The ratio of the length of the first ra-dial to the length of the first basibranchial.

10. This character is expressed as the ra-tio of the length of the first ceratobranchial to the total length of the first branchial arch.

11. The ratio of the length of the first ceratobranchial to the length of the epibran-chial.

12. The ratio of the length of the second ceratobranchial to the first ceratobranchial.

13. The ratio of the length of the second ceratobranchial to the length of the first branchial arch.

14. The ratio of the length of the hyo-branchium to the distance between the men-tal symphysis and the sternum.

15. The ratio of the anteroposterior length of the second basibranchial to its side-to-side width.

16. The ratio of the length of the cerato-hyal to the length of the entire hyobran-chium.

17. The ratio of the width of the cera-tohyal to its length.

18-22. These characters are the percent-ages of ossification of the first basibranchial, second basibranchial, first ceratobranchial, ceratohyal, and epibranchial, respectively.

23. This binary character is the absence or presence of a definite line of articulation between the first radial and the first basi-branchial.

24. The absence or presence of a definite line of articulation between the second radial and the first basibranchial.

25-27. This is a binary character with three different attributes. Each first basibran-chial either is or is not truncate, pear shaped,

or shield shaped. Column 25 on Table 3 indi-cates whether or not it is truncate; column 26 indicates whether or not it is pear shaped; and column 27 indicates whether or not it is shield shaped.

28. The absence or presence of a joint midway along the first radial cartilage.

29. A binary character based on whether or not the first radial tip attaches to the cera-tohyal.

30-31. This binary character has two at-tributes—whether the otoglossal is or is not annular in shape and whether it is or is not platelike in shape.

32. This character is whether the otoglos-sal is lightly ossified, as in *Dicamptodon*, or completely cartilaginous. The ossified condi-tion is designated with a 1 on Table 3, and the cartilaginous condition is designated with a 0.

33. This binary character is whether or not the otoglossal is fused with the second radials.

34-35. The posterior tip of the second ceratobranchial articulates with the first bran-chial arch at a point either directly on the joint between the first ceratobranchial and the epibranchial or at a point slightly poste-rior to that point. The first attribute of this character is whether or not the point of artic-ulation is posterior to the joint. The second attribute is whether or not it is directly on the joint.

36-38. This binary character has three at-tributes. The second basibranchial either is or is not triradiate, it either is or is not 4-radi-ate, and it either is or is not an inverted V.

39. This is a binary character concerned with hypertrophy or lack of hypertrophy of the levator mandibulae.

40-42. This character has three attributes concerned with the insertion of the rectus cervicis superficialis—whether this muscle does or does not insert only on the first basi-branchial, whether it does or does not insert only on the first ceratobranchial, and whether it does or does not insert on both the first basibranchial and the first ceratobranchial.

43-45. The hebosteoypsiloideus originates on one of the three myosepta posterior to the second basibranchial. These three attributes are whether or not this muscle originates on the first, second, or third myoseptum.

46. This character is the absence or pres-ence of the hyoglossus.

47. This character is whether or not there is an opening in the intermandibularis posterior at the point of the chin.

48. This is a binary character concerned with the width of the linea alba. If it is a thin line running down the midline of the throat, it is designated with a 1. If it is wider than this, it is designated with a 0.

49-50. This character deals with the number of inscriptions on the rectus cervicis superficialis. Each animal has either two inscriptions or three inscriptions.

51-52. The insertion of the rectus cervicis profundus is either fleshy or tendonous. Attribute 51 is either fleshy or not fleshy, and attribute 52 is either tendonous or not tendonous.

53-54. This character is whether the joint between the first ceratobranchial and the epibranchial is distinct or indistinct.

55. A binary character concerned with whether or not the anterior end of the geniohyoideus is overlapped ventrally by the genioglossus.

56. This character is whether or not the intermandibularis posterior is divided.

57. This is the presence or absence of parotid glands and a glandular ridge on the tail.

58-59. This character has two attributes—either the ventral edge of the tail is rounded or it is thin.

60. This is whether the genioglossus does or does not insert on the first ceratobranchial.

61. This character is whether the subhyoideus inserts on the mandible or not.

62-63. In *Dicamptodon* the majority of the hyobranchium is uniformly, but lightly, ossified or mineralized. In all of the other species the majority of the elements of this structure are cartilage. This character is whether the hyobranchium is like that of *Dicamptodon*, or whether it is mostly cartilaginous.

The numeric characters were tested for homogeneity of variance using Bartlett's Test (Dixon and Massey, 1969). Unfortunately, there was for each character in the cluster analysis at least one species in which the variance was great enough to cause heterogeneity. For this reason the numeric characters were of little use in the deduction of a phylogeny. In other words, the variation between individuals of a single species with reference to a given numeric character was so excessive that the use of this character to separate species was invalid. There is

considerable individual variation in the lengths and widths of the separate components of the hyobranchial skeleton. Other workers have used a few of these dimensions for studies at the generic level(Özeti and Wake, 1969); however, this study has shown that they are of little use in separating species or subspecies.

There were 26 binary characters used in the cluster analysis. The dendrograms for this analysis are shown in Figures 18 and 19. A brief discussion and summarization of the results of the binary characters is as follows:

Dicamptodon remains separate from the others in this analysis. It is the only species with a segmented radial, a platelike otoglossal, a fused otoglossal-second radial, no hyoglossus, no opening in the intermandibularis posterior at the chin, and a uniformly, but lightly, ossified hyobranchium.

Rhyacotriton has a totally cartilaginous hyobranchial skeleton. This is probably an advanced condition associated with terrestrial feeding habits (Regal, 1966). A cartilaginous hyobranchium is more flexible than a bony one, and in the act of feeding is a more pliable part of the tongue apparatus enabling the tongue to be extended with more speed and precision than could be done with a hyobranchium of bone. Bony hyobranchial elements are characteristic of primitive aquatic salamanders.

Another advanced trait found in *Rhyacotriton* is the reduced number of myosepta on the rectus cervicis superficialis. The number is two in this case as compared to the usual three. A trait peculiar to *Rhyacotriton* is the long subhyoideus. In all of the other species investigated this muscle is attached to the anterior end of the ceratohyal, whereas in *Rhyacotriton* it extends forward beyond that point to reach the mandible. In most of the others, the subhyoideus is so reduced as to be difficult to detect upon dissection. It has been completely overlooked by some anatomists, as pointed out above. The genioglossus is also longer than in other species, extending as far posterior as the first ceratobranchial.

The affinity between *Dicamptodon* and *Rhyacotriton* which has been suggested by numerous workers is based on data other than throat morphology. Dunn (1940) says that these two genera are related to each other and differ from *Ambystoma* in their skull features. Tihen (1958) suggested, on the other hand, that *Dicamptodon* and *Rhyacotriton*, based on the osteology of their skulls, were derived independently from the proto-ambystomatid stock and that they are different from each other and from the remainder of the family. Noble (1927), in attempting to support the idea that *Dicamptodon* and
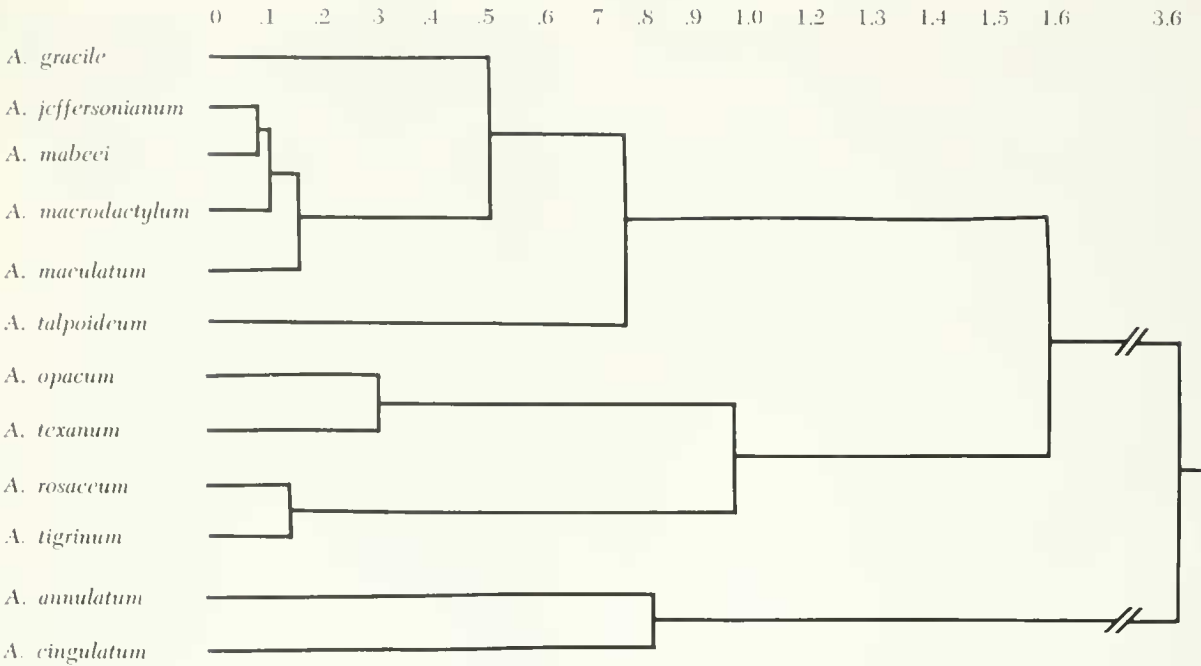
Fig. 18.   Dendrogram for the Genus *Ambystoma*.

Rhyacotriton are related, has pointed to the fact that these two genera have stream-type larvae in contrast to the pond-type larvae of *Ambystoma*. We can add to this the fact that the adults of these two stream-type genera have hypertrophied levator mandibulae muscles which are apparently of great value in grasping and swallowing the elusive types of food items present in a fast-moving stream. It is also noteworthy that in the mouth of one of the *Rhyacotriton* specimens was found a winged insect the size of a small bee. Furthermore, the geographical distributions are basically the same. They are found in the Pacific Northwest and nowhere else. In addition, the long subhyoideus in *Rhyacotriton* is a primitive trait. In spite of this, however, our studies have verified the fact that these two genera are different from each other and from the genus *Ambystoma*. Not only is *Rhyacotriton* distinct from *Ambystoma*, but it is also different from *Dicamptodon* in its wholly cartilaginous hyobranchium, fewer transverse inscriptions in the rectus cervicis muscles, unsegmented radials, annular otoglossal, and presence of the hyoglossus. We believe, therefore, that there is a preponderance of evidence for an independent derivation of *Dicamptodon* and *Rhyacotriton* from the proto-ambystomatid stock.

A. *annulatum* and A. *cingulatum* consistently remained together throughout the analyses. They share several characters. They are the only species in which the second basibranchial is 4-ra-

diate and they alone have tendonous insertions of the rectus cervicis profundus. They and *Dicamptodon* are the only species in which the first ceratobranchial-epibranchial point is indistinct. It is interesting to note that Cope (1887) considered A. *annulatum* and A. *lepturum* (*cingulatum*) to be a distinct and separate group from the other ambystomids.

As expected, the *tigrinum* group remained together, but it is of interest that A. *rosaceum* is aligned closely with them. This is a confirmation of the idea which others have expressed concerning the close relationship between A. *rosaceum* and A. *tigrinum* (Anderson, 1961). We definitely believe that *rosaceum* separated early from the *tigrinum* group and became a mountain type of tiger salamander. With the dispersion after the recent ice age salamanders of the *tigrinum* group (or their ancestral stock) in the southern areas, particularly those of the Rio Concha and other smaller drainage basins flowing into the Rio Grande, moved up the streams to become mountain inhabitants. Such a dispersal produced mountain islands of isolation with wide desert flats to insure the separation. *Ambystoma rosaceum* is also similar to some of the subspecies of *tigrinum* in its basic habitus, color (light spots or with light mottling as seen in specimens from the border states) and is a burrower. On the basis of our data this salamander should perhaps be realigned as a subspecies of A. *tigrinum*.
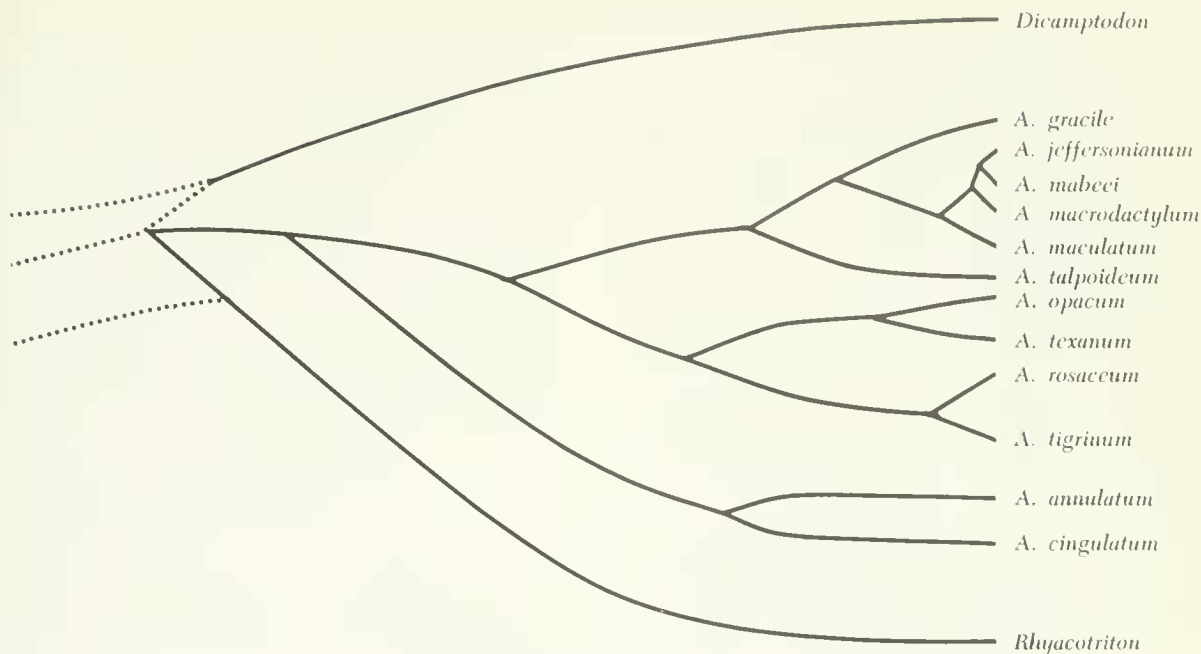
Fig. 19.   Possible phylogeny for the Ambystomidae of the United States and northern Mexico.

A. *opacum* and A. *texanum* show a closer relationship to each other on the basis of their throat anatomy than they do to other members of the family. They differ from each other in only two characters, and for the one character (the shape of the second basibranchial) they are different from all of the others. The nearest association of the *opacum-taxanum* group is with the *rosaceum-tigrinum* group at .991 (Fig. 18).

A. *jeffersonianum*, A. *mabeei*, and A. *macrodactylum* differ in none of the binary characters. However, A. *macrodactylum* can be separated from A. *jeffersonianum* and A. *mabeei* by the fact that it contains no ossification in the epibranchial tips in fully transformed adults. A. *jeffersonianum* and A. *mabeei* can be separated by the shapes of their otoglossal cartilages (Fig. 6 and 7). A. *maculatum* differs from the others in the width of the linea alba. A. *gracile* is associated with this same cluster, differing from them in the shape of the first basibranchial and in having a divided intermandibularis posterior.

A. *talpoideum* is aligned more closely with the   gracile - jeffersonianum - mabeei - m a c r o-dactylum-maculatum group than with the *opacum-texanum-tigrinum* group. This is based primarily on the shape of the first basibranchial. The former group, like A. *talpoideum*, all have pear-shaped first basibranchials, whereas this structure in the latter group is shield shaped.

When the binary characters concerned with muscles are masked from the analysis, the alignment of the species is unchanged from that described above. This then, represents an arrangement based on the hyobranchial skeleton. The hyobranchial skeleton characters were also masked, and the analysis produced thereby is one based on information concerning muscles. In this case A. *opacum* and A. *texanum* are more widely separated from each other than in the former method, and A. *rosaceum* becomes more widely separated from the *tigrinum* group. Otherwise, the cluster arrangement is the same. Such confirming data derived from two anatomical sources add considerable weight to a phylogenetic conclusion and seems to us to be of utmost importance.

There is considerable similarity between the alignment of the species of the genus *Ambystoma* as presented here and that suggested by Tihen (1958). There is agreement in the placement of A. *rosaceum* in the *tigrinum* group, and in the placement of A. *gracile*, A. *jeffersonianum*, A. *macrodactylum*, and A. *maculatum* in the *maculatum* group. He has also aligned A. *annulatum* and A. *cingulatum*. We disagree in the placement of A. *talpoideum*, A. *mabeei*, and A. *texanum* (compare Figure 18 with Tihen's groups in the introduction).

Tihen's classification is based on skull morphology, whereas ours is based on the hyobranchial apparatus. Inasmuch as the hyobranchial apparatus is more directly involved with those anatomical structures asociated with the processes of breathing and feeding than is the skull, this apparatus provides, we believe, a more sensitive

indicator of the evolution that has occurred in these salamanders.

Some interesting evidence with regard to interfamilial relationships has come to light in the course of this investigation. Most workers are of the opinion that the ambystomids gave rise to the salamandrids and that the salamandrids in turn gave rise to the plethodontids. Regal (1966), in considering feeding mechanisms, affirms that the free-tongue condition seen in the plethodontids is an advanced condition and that the tongue of the Salamandridae, which is attached and less protrusible, is a correspondingly less advanced condition. He further concludes that in primitive salamanders the tongue, being firmly attached at its base and along its sides, is not capable of extension outside of the mouth cavity. This latter type is an aquatic structure—a "water tongue"—whereas the free-tongue condition is found in terrestrial salamanders which feed upon more elusive prey. For the most part the Ambystomidae have a tongue which is attached in a primitive manner. The flexible hyobranchium of *Rhyacotriton*, however, enables this advanced ambystomid to utilize terrestrial feeding more so than it would appear to occur in most of the other members of the family. The long subhyoideus and genioglossus muscles have assumed an important role in propelling the tongue forward.

The epibranchial cartilage was found in all of the ambystomids dissected. The absence of this cartilage in some of the salamandrids would appear to be evidence for the advanced nature of the Salamandridae with respect to the Ambystomidae.

Further evidence for this relationship is found in the fact that there were two pair of radials present in all of the ambystomid specimens. Some salamandrids have only one pair, and Bogoljusky (1924) has confirmed that the two-pair condition is primitive. The otoglossal cartilage was also present in all of the ambystomid specimens, whereas it is lacking in both Salamandridae and Plethodontidae (Dunn, 1926). Figure 17 illustrates those changes which have occurred in the otoglossal and the radials. The primitive ambystomid, *Dicamptodon*, has a platelike otoglossal which is fused to the second radials. The more advanced condition in Ambystomidae consists of an annular otoglossal which articulates with the tips of the second radials. The salamandrid condition shows complete loss of the otoglossal and in some genera a loss also of the second radial. The otoglossal is absent in Plethodontidae as illustrated in Figure 17, and there is likewise a noticeable reduction in the radial cartilages. As the tongue has become more flexible and freed from the floor of the mouth in

advanced salamanders, it would appear that there has been a tendency toward reduction and even loss of the otoglossal as well as a rearrangement of teeth over the roof of the mouth. The rearrangement consists of a shifting of the teeth posteriorly to lie directly above the tongue pad rather than more anteriorly to correspond in position above the otoglossal as in the ambystomids. In the more terrestrial salamandrids and plethodontids, the tongue has become increasingly freed from the floor of the mouth and functions more effectively in the capture of insects. Captured insects are manipulated by the tongue and forced up against the numerous teeth located on the roof of the mouth. Ambystomids, on the other hand, have a much less flexible tongue, and have retained the otoglossal cartilage apparently as an aid in forcing food up against the vomerine teeth, which form a transverse row directly opposite the otoglossal.

The epibranchial is longer with respect to the ceratobranchial in Salamandridae (Özeti and Wake, 1969) than in the Ambystomidae studied. Tanner (1952) illustrated these extremely long cartilages in the Plethodontidae.

The second basibranchial is present in all of the ambystomids studied. It is lost in most salamandrids (Özeti and Wake, 1969) and is probably completely missing in plethodontids (Dunn, 1926; Tanner, 1952).

All of the foregoing facts support the hypothesis that the ambystomids are primitive to the salamandrids and that the latter are in turn primitive to the plethodontids. There is reason, however, to consider another alternative. If ossification of the hyobranchium is to be considered a primitive character, then with respect to this character the Salamandridae would be primitive to the Ambystomidae and the Plethodontidae. The ceratohyal, for example, is from 30 to 50 percent ossified in most salamandrids (Özeti and Wake, 1969), whereas it is much less than this in Ambystomidae (Table 1) and in the Plethodontidae (Tanner, 1952; Wake, 1966). The first ceratobranchial is totally unossified in the Ambystomidae and well ossified in most Salamandridae. However, there are salamandrids with totally cartilaginous hyobranchial skeletons, and, therefore, since this high level of ossification is not consistent throughout the family, the use of percentages of ossification as an index of phylogenetic relationships between families seems to be unjustified. In fact, there is considerable variation within each family with respect to percentages of ossification, and, moreover, an interesting parallelism seems to have occurred in each family. The advanced members of a particular family seem to be more capable of terrestrial

feeding habits, and in these salamanders there has been a reduction in the amount of calcification in the hyobranchium, thereby making it more flexible to facilitate the capture of prey through tongue pad flipping. The highly advanced free-tongued plethodontids studied by Tanner (1952) were shown to have no ossification whatever in the hyobranchium, whereas the more primitive plethodontids as reported by Wake (1966) did have definite centers of bone in the hyobranchium. The ambystomid which is most terrestrial in its feeding habits, *Rhyacotriton*, has a completely bone-free hyobranchium; and the terrestrial feeders among the Salamandridae (*Salamandra*, *Chioglossa*, and *Salamandrina*) are likewise equipped with more cartilage in the hyobranchium than the other presumably more primitive members of the family (Özeti and Wake, 1969). It would appear, therefore, that the percentage of ossification of the hyobranchium may have some value as an index to phylogeny, but is of limited value if one wishes to study interfamilial phylogeny. Thus, the percentage of ossification has importance in determining the degree of adaptation toward a terrestrial habitat.

An investigation of the muscle adaptations is also important and of interest in an assessment of development toward the more terrestrial type of feeding. An examination of the more advanced plethodontids indicates a greater development of the anterior transverse muscles. Except for the genus *Thorius* those genera of free-tongue plethodontids studied by Tanner (1952) possessed a large anterior development of the intermandibularis. According to his analysis, this represents the intermandibularis anterior, a muscle thought by Piatt (1935) to be lost at metamorphosis. This must yet be demonstrated by an embryological investigation; however, the fact still remains that in these plethodontids there is a relatively large mass of transverse muscle which ties the anterior part of the mandibular area together and which is not interrupted by the linea alba. The development anteriorly is also accompanied by a reduction in the size and extent of the transverse muscles in the more posterior areas of the throat.

If we examine other related but more primitive families (salamandrids and ambystomids), we do not see the same types of muscle development; but we do see in the more terrestrial forms of these families a development of the more anterior transverse muscles. In the Salamandridae, for example, the genera in which terrestrial feeding is best developed are *Salamandra*, *Chioglossa*, and *Salamandrina*; and, furthermore, these three genera tend to have a greater degree of elaboration of the anterior portions of the throat musculature than other genera in the family (Özeti and Wake, 1969). There is also a concomitant reduction in the posterior parts of the throat musculature in these land feeders. The three genera of salamandrids noted above all have experienced a reduction in myosepta of the rectus cervicis superficialis as compared to the other members of the family, and a corresponding reduction in rectus cervicis superficialis myosepta has occurred in *Rhyacotriton* of the *Ambystomidae*.

In the plethodontidae there is also a reduction of the myosepta in the rectus series. Tanner (1952) figures this reduction and also indicates a reduction and finally a complete loss of the omohyoideus muscle, which in the less advanced species ties the rectus throat muscles to the pectoral girdle (scapula). There is also a gradual reduction in the size of the second basibranchial (os thyroideum) until it is lost in the free-tongued plethodontids. These reductions and deletions have also served to increase the flexibility of the longitudinal throat muscles and have produced an uninhibited band of muscle from the pelvis to the hyobranchium providing a mechanism for rapid tongue retraction.

An analysis of the myology and osteology of the hyobranchium of the families Ambystomidae, Salamandridae, and Plethodontidae provides evidence to support the conclusion that there has been a degree of parallel development leading toward a terrestrial development of feeding and perhaps breathing. In all three families, we note a reduction in the ossification of the skeletal elements of the hyobranchium depending, we believe, on the degree of the terrestrial type feeding achieved by members of a generic or specific group within these families. The flexibility of the hyobranchium achieved by the free-tongued plethodontids is most remarkable and has virtually eliminated in some species that type of feeding in which jaws are used as the grasping or food-getting device. One is caused to wonder if the development of the tongue as an almost exclusive food-getting device is the ultimate type of development to be achieved in the process of adaptive radiation in terrestrial salamanders and perhaps also in lizards (Chameleonidae).

The conversion of the skeletal elements into a flexible cartilaginous structure and the reduction in size and deletion of some elements has been accompanied by modifications in the myology. As indicated above, there have been basic modifications in the muscles which have in effect reduced the heavy musculature of the throat area. Associated with this reduction, there has

been a specialization in both the transverse and longitudinal muscle series. A specialization of particular interest to us is the development of the most anterior transverse muscles in certain groups of each family in which the muscle fibers extend uninterrupted across the midline. Tanner (1952) referred to these as the intermandibularis anterior and based his conclusions on the fact that in the plethodontids studied there was a small tendinous fascia tying each end of the muscle to the opposing mandible. A comparison of this muscle in those ambystomids and salamandrids in which fibers extend across the linea alba suggests that in these families those continuous fibers represent the anterior fibers of the intermandibularis posterior which have been modified to strengthen the anterior area of the now changing food-getting mechanism. We have found no indication that the intermandibularis anterior is retained in any members of the latter two families. This anterior myological specialization suggests that there is a definite convergence leading toward a terrestrial type of feeding which involves an increasing use of a more flexible tongue.

If we examine the posterior transverse muscles, we note a reduction in size and mass with an increase in the width of the central fascia as the entire structure becomes more flexible. The longitudinal series has also been effected to the extent that they have become more elongate (in some plethodontids the rectus cervicis series are actually folded, Tanner, 1952, plate 73, Fig. G). Özeti and Wake (1969) indicate a reduction in the numbers of myosepta in the rectus series of such genera as *Salamandra*, *Chioglossa*, and *Salamandrina*. We partcularly note a similar change in *Rhyacotriton* in which the myosepta of the rectus series have been reduced to two. In *Rhyacotriton* the genioglossus has been extended beyond the first radii of the first basibranchial and reaches posterior to insert on and in fascia attached to the first ceratobranchial. This adaptation provides for a longer muscle and permits a greater length of contraction in pulling the hyobranchium anteriorly in the extending of the tongue. Although we note that different structures have been altered, the general effect appears to be the same, namely, that terrestrial groups in each family have modified the hyobranchium to provide for greater flexibility and have increasingly involved the tongue as an evermore important food-getting organ.

We have found the musculature of the Ambystomidae to be more advanced in some respects than previous workers have reported. Contrary to Piatt's findings, the ambystomids do have a subhyoideus, and therefore this character cannot be used to separate the families as it has been in the past. Piatt further reported that the transverse ventral throat muscles posterior to the intermandibularies posterior are the interhyoideus posterior in Crytobranchidae, Amphiumidae, and Ambystomidae and that these two muscles remain in the adults in an essentially unchanged condition. We have found the interhyoideus posterior to be the same as the larval muscle. In the Plethodontidae, this muscle becomes divided into the gularis and the quadratopectoralis. The interhyoideus of the larva, however, becomes divided into subhyoideus and interossaquadrata in the adults of Ambystomidae and Salamandridae.

This new information on myology does not answer the question with regard to the relationship between Ambystomidae and Salamandridae except that it does make the ambystomids appear more advanced than they were previously thought to be. The preponderance of evidence still seems to support the concept that the Ambystomidae are primitive to both the Salamandridae and the Plethodontidae.

In the past it has been assumed that the order of phylogeny is from the Ambystomidae to the Salamandridae to the Plethodontidae. However, based on the findings of this study there is a second distinct possibility that the ambystomids may have given rise independently to both the salamandrid and plethodontid families. These two possibilities are presented in Figure 20.

SUMMARY

1. The hyobranchial skeleton is mostly cartilaginous with a few isolated areas of bone located in certain components. Only in *Dicamptodon* is ossification widespread throughout the hyobranchium, although this ossification is not heavy. In only a few areas in *Dicamptodon*, such as the tips of the ceratohyals, is the ossification heavy.

2. The first basibranchial is shield-shaped, pear-shaped or rod-shaped and usually has a central core of bone. Bone is completely absent in *Rhyacotriton* and in *A. gracile*.

PLETHODONTIDAE

↑

SALAMANDRIDAE

↑

AMBYSTOMIDAE

✦ ✦ ✦ ✦ ✦

SALAMANDRIDAE   PLETHODONTIDAE
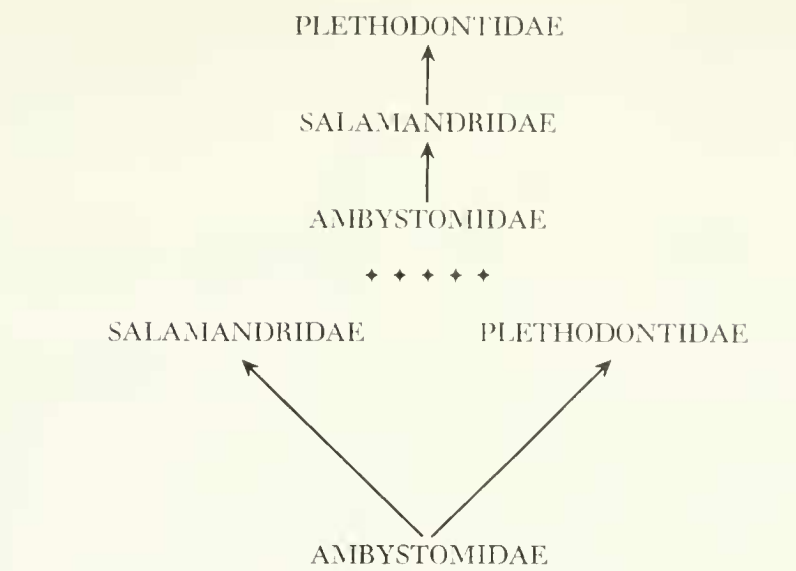
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AMBYSTOMIDAE

Fig. 20.   Diagrams depicting the possible phylogenetic relationships between the Ambystomidae, Salamandridae, and Plethodontidae.

3. The first radial cartilages are entirely cartilaginous. They are usually long, slender rods that may or may not unite with the tips of the ceratohyal; although in *A. cingulatum* they are very short and rounded. In *Dicamptodon* there is a joint midway along the length of the first radial.

4. The second radial cartilages are always unossified and curve dorsally to meet the otoglossal. *Dicamptodon* has a fusion of the second radials and the otoglossal plate to form a single platelike structure.

5. There is usually no ossification in the first ceratobranchial. One specimen of *A. cingulatum* contained a spot of bone in the medial end of this structure which represented 11 percent of the total volume of the first ceratobranchial.

6. The second ceratobranchial is always unossified and articulates with the first branchial arch either at the joint between the first ceratobranchial and the epibranchial or immediately posterior to that joint.

7. There is an epibranchial cartilage in all species included in this study. However, in some the articulation of this structure with the first ceratobranchial is indistinct. This is the case in *Dicamptodon, A. annulatum,* and *A. cingulatum.*

8. The ceratohyal is often ossified on its posterior or distal tip.

9. The second basibranchial is present in all species. Its shape is 3-radiate, 4-radiate, or an inverted V. Usually, the central portion is ossified with the tips of the lateral arms remaining cartilaginous. In *Dicamptodon, Rhyacotriton,*

and *A. opacum,* the entire structure is cartilaginous.

10. The linea alba is usually wide at the level of the intermandibularis posterior. In *A. maculatum* it is a very thin line.

11. The fibers of the intermandibularis posterior insert into the linea alba of the throat; although, in *Rhyacotriton, A. cingulatum,* and *A. gracile,* a few of the anterior fibers extend all the way across the midline without being interrupted by the linea alba.

12. The levator mandibulae is hypertrophied in *Rhyacotriton* and *Dicamptodon.* This may be associated with their stream feeding habit, which requires a more aggressive behavior than used by the other members of the family (genus *Ambystoma*) in their pond habitats.

13. Contrary to the reports of earlier workers, the subhyoideus is found in all species studied. It is derived from the larval interhyoideus which at metamorphosis divides into the subhyoideus and the interossaquadrata. It is usually small and delicate and extends forward only as far as the anterior edge of the ceratohyal. In *Rhyacotriton,* however, it is longer, extending all the way forward to the mandible. In *Dicamptodon,* this muscle is not as long as in *Rhyacotriton,* but it is thick and heavy when compared with other species.

14. The genioglossus is divided into a ventral and dorsal portion in all species. Only in *Rhyacotriton* does this muscle extend as far posteriorly as the first ceratobranchial.

15. A hyoglossus is present in all species ex-

cept *Dicamptodon*. The posterior portion of the genioglossus in *Dicamptodon* lies in the position occupied by the hyoglossus in the other members of the family, and it appears likely that the hyoglossus is derived from the genioglossus by specialization of the posterior part of the muscle.

16. There are usually three transverse inscriptions on the rectus cervicis superficialis. In *Rhyacotriton* and *A. talpoideum*, however, there are only two.

17. The rectus cervicis profundus usually attaches to the otoglossal cartilage by a fleshy rather than a tendonous insertion. In *A. annulatum* and *A. cingulatum* this insertion is by way of a thin tendon.

18. The hebosteoypsiloideus originates on the second myoseptum of the rectus cervicis profundus posterior to the second basibranchial in all species except *A. annulatum* and *A. opacum*, in which it arises from the first inscription.

19. The variation in ratios of dimension of hyobranchial skeleton elements that is found within a given species is excessive beyond that which would allow this information to be of value in species differentiation. Whereas these dimensions have been used successfully by other workers in the phylogenetic alignment of salamanders at the generic level, this study indicates they are not equally usable in studies at the species level.

20. The 16 species and subspecies are placed into six groups according to their throat morphology as follows: The *Dicamptodon* group, the *Rhyacotriton* group, the *A. annulatum-A. cingulatum* group, the *A. gracile-A. jeffersonianum- A. mabeei-A. macrodactylum-A. maculatum* group, the *A. talpoideum* group, the *A. opacum-A. texanum* group, the *A. rosaceum- A. t. tigrinum-A. t. melanostictum- A. t. nebulosum* group.

21. *Dicamptodon* appears to be the most

primitive group, and *Rhyacotriton*, the most specialized.

22. Based on the morphology of the throat region, it is suggested that *A. rosaceum* be placed in the tiger salamander group as a subspecies of *A. tigrinum*.

23. The binary characters when applied separately to the hyobranchial skeleton and the hyobranchial musculature produce essentially the same phylogenetic results.

24. In comparing the hyobranchium and throat myology in different families of salamanders, there appears to have developed a parallelism within each family with respect to adaptations toward terrestrial feeding. These adaptations include the reduction and even complete loss of bone in the hyobranchium. The elaboration of the anterior throat musculature to provide a mechanism for rapid tongue pad flipping has resulted in a reduction in the size of muscles and in the number of myosepta in the posterior throat musculature. These adaptive changes seem to have occurred as the need for sucking action and jaw movement seen in aquatic salamanders are replaced by rapid tongue protrusion and retraction in the terrestrial forms.

25. The results of this investigation support the hypothesis that Ambystomidae is primitive to Salamandridae and to Plethodontidae. The findings which have led to this conclusion are based upon the protrusibility of the tongue and upon the structure and presence of the epibranchial, otoglossal, second radial, and second basibranchial cartilages of the three families. The muscles which have added information concerning these interfamilial relationships are the intermandibularis posterior, levator mandibulae, subhyoideus, genioglossus, hyoglossus, rectus cervicis profundus, rectus cervicis superficialis, and hebosteoypsiloideus.

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